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## FISHING WITH THE CORMORANT. I. IN CHINA

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THE chief flesh food in the erstwhile Celestial Empire consists of the fish found in the streams and canals which everywhere abound. To catch these fishes, the Chinese have probably devised more interesting and ingenious apparatuses than any people in the world. It is my purpose later on to describe some of the more extraordinary of these devices, but this article will be restricted to the use of a bird, the cormorant, as a fish-taker.

Nearly every one who has travelled in China (and his name is legion) has written a book on his travels, and practically every book of travels in the south of China especially contains an account of cormorant-fishing. It is not my purpose in this article to bring together and quote or even synopsise these many accounts. This would surely be a work of supererogation, since every account of this phenomenon among the Chinese is, save for details, essentially a duplicate of every other account—the process to-day being practically that described in the earliest printed works on China. This is in part due to the fact that the practice has been well worked out, and in part also to the fact that the Chinese are a people firmly wedded to the habits of their ancestors. So instead of quoting or even synopsizing all these accounts my plan is to bring together all the oldest accounts and especially the oldest figures (all too few in number) of

this interesting fishing method, and then to bring in some modern accounts which present interesting features, and finally to conclude with some figures illustrating present-day scenes in the carrying on of this fishing.

The oldest and the most interesting printed accounts came to me while I was compiling the section of Pre-Linnaean literature of fishes for volume III of the "Bibliography of Fishes." An effort has been made to get all these early accounts, but of later works I have taken only such as have come to hand without any particular search.

One of the first European travelers and describers of China was Marco Polo, and his great work—especially in the Yule-Cordier edition of 1903—is a wonderful thesaurus of things Chinese for the years 1275–1292, during which time Polo lived in and traveled throughout Cathay. His book abounds in most interesting and valuable natural history observations, but one is surprised to find among them no reference to cormorant-fishing. Not so, however, Odoric of Pordenone, whose sojourn in China covered three years somewhere between 1323 and 1328. In his book (1513) is found the earliest printed account of fishing with the cormorant.

However, cormorant-fishing as practised in China during Odoric's visit was no new thing but was a custom that goes back into the remote history of the Middle Kingdom. Unfortunately, I have found no accounts in which to trace backwards this undoubtedly ancient practice among the Chinese. In discussing this point with Dr. Clark Wissler, curator of anthropology in the American Museum, he suggested that I write the distinguished Sinologist, Dr. Berthold Laufer, curator of ethnology in the Field Museum, Chicago. This I did and am privileged to quote from his reply as follows: "From the available evidence we can only infer that cormorant-fishing was established under the Sung dynasty (960–1298) and in Japan possibly a little earlier (end of 6th century). The practice seems to have originated in Che-

kiang and Kiang-su and to have spread from there to other provinces." It is to be hoped that Dr. Laufer will shortly publish his researches on this obscure but interesting subject.

But let us return to our old traveler and read his account, the first on record in Europe, of this very unusual phenomenon. His book was first published at Pesaro, Italy, in 1513 under the title—"Odorichus De Rebus Incognitis." The next edition was a French version at Paris, 1529, "*L'Hystoire Merveilleuse*," etc. Next came two Italian versions from different manuscripts published by Ramusio<sup>1</sup> in his "*Navigazioni et Viaggi*," volume II, Venetia, 1583. The fifth and sixth editions and versions, one in Latin and one in English, were made and published by Richard Hakluyt<sup>2</sup> in 1599. His English version (the first ever made) reads as follows:

And from thence, I traueiled 18. dayes iourney further, and came vnto a certaine great riuer, and entered also into a city, whereunto belongeth a mighty bridge to passe the said riuer. And mine hoste with whom I sojournd, being desirous to shew me some sport, said vnto me: "Sir, if you will see any fish taken, goe with me." Then hee led me vnto the foresaid bridge, carying in his armes with him certaine diue-doppers or water-foules, bound vnto a company of poles, and about euery one of their necks he tied a threed, least they should eat the fish as fast as they tooke them: and he caried 3. great baskets with him also: then loosed he the diue-doppers from

<sup>1</sup> In one of Ramusio's versions, the fishing incident is almost entirely omitted, and in the other the agent is called *marigione* or *sea-calf* and is plainly the otter. Furthermore, Sir John Mandeville, who "cribbed" this story from Friar Odoric, calls the beast *loir* or *loutre*, the otter. Both the cormorant and otter accounts are probably correct as I hope to show later in an article on fishing with the otter. In Cordier's French version of Odoric (Paris, 1891) the word "*plungons*" is used.

<sup>2</sup> Hakluyt, Richard. "Here Beginneth the 'Journal of Frier Odoricus . . . Concerning Strange Things Which Hee Sawe Among the Tartars of the East.'" (In his "*The Principal Navigations, Voiages, Traffiques, and Discoueries of the English Nation, made by Sea or ouer-land, to the remote and farthest distant quarters of the Earth, at any time within the Compassee of these 1500 yeeres*," etc., London, 1599, vol. II, pp. 53-67. Reprinted, London, 1810. Also in the Maclehose reprint of the "*Principal Navigations*," Glasgow, vol. IV, 1904, p. 425. Also reprinted almost literally as an appendix to John Ashton's edition of "*The Voiage and Travayle of Sir John Mandeville, Knight*," etc., London, 1887. This is done under its own title and not as a part of Mandeville. The account of fishing with cormorants is found on pp. 241 and 242.

the poles, which presently went into the water, & within lesse then the space of one houre, caught as many fishes as filled the 3. baskets: which being full, mine hoste untied the threeds from about their neekes, and entering the second time into the riuer, they fed themselues with fish, and being satisfied they returned and suffered themselues to be bound vnto the saide poles as they were before. And when I did eate of those fishes, me thought they were exceeding good.

The "dive-doppers" are of course cormorants, but as to the "company of poles" to which the birds were tied, I can only suggest that these made up a bamboo raft from which the fishing was probably conducted. As will be pointed out (Staunton's and Malpière's accounts on pages 19 and 20) the fishermen sometimes carry to the river a light boat with the birds tied fast to the gunwales and they could even more easily carry the light bamboo rafts with which much of the cormorant-fishing is carried on.

Colonel Yule's fine translation of Ordoric in Cordier's revision<sup>3</sup> reads as follows:

Passing hence, and travelling for eighteen days more, through many cities and towns, I came to a certain great river, and I tarried at a certain city [called Belsa] which hath a bridge across that river. And at the head of the bridge was a hostel in which I was entertained. And mine host, wishing to gratify me, said: "If thou wouldst like to see good fishing, come with me." And so he led me upon the bridge, and I looked, and saw in some boats of his that were there, certain water-fowl tied upon perches. And these he now tied with a cord round the throat that they might not be able to swallow the fish which they caught. Next he proceeded to put three great baskets into a boat, one at each end and the third in the middle, and then he let the water-fowl loose. Straightway they began to dive into the water, catching great numbers of fish, and ever as they caught them putting them of their own accord into the baskets, so that before long all the three baskets were full. And mine host then took the cord off their necks and let them dive again to catch fish for their own food. And when they had thus fed they returned to their perches and were tied up as before. And some of those fish I had for dinner.

What this city Belsa was neither Yule nor Cordier can conjecture. This name is interpolated in Ramusio's minor version, to which reference has been made previously.

<sup>3</sup> Yule, Sir Henry. "Odoric of Pordenone," Vol. II, of "Cathay and the Way Thither" [in 4 vols., Hakluyt Soc., series II], (Translated and edited by Sir Henry Yule: new edition revised with notes by Henry Cordier). Hakluyt Soc., 1913, Series II, vol. xxxiii, pp. 188 to 190.



The next author known to report the use of the cormorant for fishing in China is Galeotto Perera<sup>4</sup> (1577). Of the sources of his account nothing is known save the statement in the English version by R. Willes in Eden's book of 1577 that this translation is made directly from the Italian. Even the expert bibliographers of the Library of Congress have been unable to throw any light on the matter. Perera's observations were made in the province of "Chenchi" (Shensi?). Willes's translation reads as follows:

I have seene in this ryuer (near Goa) a pretie kynde of fyshyng, not to be omitted in my opinion, and therefore wyll I set it downe. The Kyng hath in many ryuers good store of barges full of sea crowes, that breede, are fedde, and do dye therein, in certayne cages, allowed monthly a certayn prouision of ryse. These barges the kyng bestoweth uppon his greatest magistrates, geuyng to some two, to some three of them, as he thynketh good, to fyshe therewithall after this maner. At the houre appoynted to fyshe, all the barges are brought together in a circle, where the ryuer is shalowe, and the crowes, tyed together under the wynges, are let leape downe into the water, some under, some aboue, worth lookyng uppon; eche one as he hath filled his bagge, goeth to his owne barge and emptieth it, whiche done, he retourneth to fyshe agayne. Thus hauyng taken good store of fyshe, they set the crowes at libertie, and do suffer them to fyshe for theyr own pleasure. There were in that citie, where I was, twentie barges at the least of these aforesaid crowes. I wente almost euery day to see them, yet coulde I never be thoroughly satisfied to see so straunge a kynde of fyshyng.

The distinctive feature of this report is that the wings of the cormorants are tied by a cord passing over the back and under their basal joints. Undoubtedly this is to prevent their flying away. Later authors report the same fashion of tying the birds, but this is the earliest known reference.

Juan Gonzalez de Mendoza<sup>5</sup> visited China in the latter half of the sixteenth century and published at Rome in

<sup>4</sup> Perera [Pereira], Galeotto. (R. Willes Trans.) "Certaine Reportes of the Province of China Learned . . . Chiefly by the Relation of Galeotto Perera, a Gentlemen . . . that Lay Prisoner in that Country many yeeres. Augmented and Finished by Richard VVilles." In Eden, Richard, "History of Travayle in the VWest and East Indies," London, 1577, p. 253. Also in the London 1810 edition of Hakluyt's "Principall Voyages, Traffiques and Discoueries." Also in Hakluyt Soc. Reprint, Extra Series, vol. vi, p. 327, 1904 (MacLehose, Glasgow).

<sup>5</sup> Gonzales de Mendoza, Juan. "Historia de la Cosas mas Notabiles, Ritas y Costumbres, del Gran Reyno dela China," etc., Rome, 1585. Another

1585 an account of his travels. An English version was made by R. Parkes and published at London in 1588. From it the following quotation is excerpted:

The king hath in euerie citie founded vpon the riuers, houses wherein euerie yeare is brought vp many cormorantes or sea rauens, with whome they doo fishe in those monethes that the fish dooth spawne, and that is in this maner following. They take the cormorantes out of their cages, and carrie them vnto the riuer side, whereas they haue many barkes ordeyned for their fishing, and they are halfe full of water.

Then they take their cormorantes, and with a corde they do binde their mawes, in such sort that no fish can fall into it: then they do cast them into the riuer to fish, the which they do with such good will and couetousnesse, that it is a woonder to see; they throwe themselves into the water with great swiftnesse, and diue, whereas they do fill their throate with fish. Then they come foorth, and with the like hast they go vnto the barkes that are halfe ful of water, and the fish which they have taken they put in that water, which is put there for that purpose, that the fish may not die; the which being done, they returne againe vnto their fishing as they did before.

In this order they do indure their fishing foure houres together, in such sort that the one doth not trouble the other; and when yt their boates with water are ful of fish, then do they vnbind them, and turne them againe into the riuer for to fish for themselues, for they haue neede thereof, for that alwayes the day before that they will fish they keepe them from their ordinarie victualles, which is a little *millio*, that they may ye better do their office. So after a while that they haue filled their bellies and recreated themselves, they take them out of the water and carrie them vnto the ordinarie places, whereas they are kept; and euerie third day during the time of this fishing, they do take them forth for the same exercise, which for them is so great pastime, that they would it should indure all the yeare.

Here for the first time we have the boat partly filled with water into which the fish are put to keep them alive and fresh for the market—a record which antedates by over a hundred and twenty-five years the earliest known account of an English boat with a well.

Next come Maffei<sup>6</sup> (1589) who notes that they put a collar of iron around the cormorant's neck which would

edition bearing same title, Madrid, 1586, p. 104. English version by R. Parke, "The Historie of the Great & Mightie Kingdome of China," etc., London, 1588, chapter xxii. This has been edited by Sir George Staunton as an almost *verbatim et literatim* reprint (spelling modernized) in the Hakluyt Soc. Works, Series I, vols. 14 and 15, London, 1853. Mendoza's account of cormorant-fishing is found in Vol. 14, pp. 154 and 155.

<sup>6</sup> Maffei, Jo. Peter. "Historiarum Indicarum, Libri XVI," Lugduni et Coloniae Aggripinae, 1589, chap. iii;—L'Ecluse, Carolus. "Exoticorum Libri Decem." Antwerp, 1605, p. 106;—De Feynes, Henri de Montfort. "Voyage Faict par Terre depuis Paris jusques à la Chine." Paris, 1630, pp. 173 and 174.

allow the small fishes to pass but not the large ones: L'Ecluse, who quotes Mendoza and seems to have no first-hand knowledge; and De Feynes (1630), who saw this fishing at Canton. None of these men, however, add anything new and they may be passed without further comment. Probably a minute search through other books of Chinese travels in the late fifteen hundreds and the first half of the sixteen hundreds, would reveal other accounts of cormorant-fishing, but the return would hardly justify the effort.

We now come to a series of accounts which are by-products of embassies, the first to Muscovy and Persia, the others to China. In the first, Crusius and Brugman were sent by the Duke of Holstein to Russia and Persia. With them went one Jean Albert de Mandelslo, who left them at Ispahan, went to Ormuz, to Seurat, travelled through central India, took ship for England and was becalmed for three weeks off Ceylon's "coral strand." During that time he talked with various officers and passengers, the latter mainly Jesuit priests returning from China and the East, and compiled that part of his work dealing with the East Indies, Japan and China.

I first thought that Mandelslo got his cormorant-fishing account from some of these travelers, but careful comparison with Mendoza's account shows it to be almost identical with this. That Mandelslo copied it himself seems hardly probable. It was probably inserted by Adam Olearius who edited Mandelslo's book. This account in question is found on page 224 of the first edition of the English version by John Davies of Kidwelly—"The Voyages and Travels of J. Albert de Mandelslo . . . into the East Indies [1638-1640]." London, 1662. (In Olearius, Adam, "The Voyages and Travels of the Ambassadors sent by Frederic, the Duke of Holstein, to the Great Duke of Muscovy and the King of Persia. Rendered into English by John Davies of Kidwelly." London, 1662). Mandelslo's work went through many editions and translations beginning with a German text, Schleswig, 1645, and coming down to a French version

by de Wicquefort at Paris in 1656. None of these have been obtainable for purposes of comparison, but Davies says that he made his translation from a large French version—probably the above.

Now come the two accounts (both illustrated) incidental to two embassies sent by the Dutch East Indies Company to the government of China. The first was written by Johan Nieuhof, a German steward in the employ of the Dutch East India Company, who accompanied Peter de Goyer and Jacob de Keyser, ambassadors from the company to the emperor of China during the years 1655-1657. Nieuhof's account of the embassy and its experiences were embodied in the first edition of his book published in Dutch at Amsterdam in 1665. This underwent many translations and publications. It was turned into English by John Ogilby and published at London in 1669. Nieuhof saw the birds at work, describes the scene in the first person and what is even more interesting to us gives the first known figure of this extraordinary method of fishing. This figure and account are reproduced in practically all these editions and versions. Here follows Ogilby's translation of Nieuhof's<sup>7</sup> Dutch work.

About this City [Nynyang] we saw them catch Fish with a Bird, which they call *Louwa*: and because this way of Fishing seems notable, and no where else used but in China, I here present you with the shape of the Fowl in the annexed cut: This Bird *Louwa* is somewhat less than a Goose, and not very unlike to a Raven; it has a long Neck, and a Bill like an Eagle.

With these they Fish after this manner; they have small Boats very Artificially made of Reeds or Bamboos with which they Sail upon the Chinese Rivers and Pools, and place the Bird perching upon the out-side of the vessel, from whence she suddenly shoots and Diving, swims under water as fast as they can thrust forward their Cobles with a light Pole. As soon as she has caught her prey, she instantly appears above water, and the Master

<sup>7</sup> Nieuhof, Johan. "Het Gezantschap Der Neerlandtsche Oost-Indische Compagnie," Amsterdam, 1665. This is the first edition, not seen by me. Another edition of like date and title from Antwerp was examined in the New York Public Library. First French version, "L'Embassade de la Compagnie Orientale des Provinces Unies vers l'Empereur de la Chine," etc., Amsterdam, 1665, is in the Library of Columbia University. English version by John Ogilby is "An Embassy from the East-India Company of the United Provinces to the Grand Tartar Cham, Emperor of China," etc., London, 1669, pp. 99 and 100.

of the Boat stands ready to receive her, and opens her bill by force and takes out the Dainty. Afterwards he turns her out again to catch more, and to prevent these Birds from swallowing down the prey, they hang a Ring about their Necks, which hinders them from gorging: Such Fish as are too big for them to bring up in their Bills, they discover to their Masters, by making a noise in the water, who then helps to pull them out.

Such Birds as are slothful and loth to Dive, are broken of that ill habit by beating. When they have caught enough for their owners, the Iron ring is taken off, and they are left to Fish for themselves, which makes them the more willing to work for others. The Fishermen pay a yearly Tribute to the Emperour for the use of these Birds, which are in much esteem with the Chinese; and such as are nimble and well taught, are so dear, that oftentimes one of them goes at fifty Toel of Silver, which is about one hundred and fifty Guilders. We offered to buy of an old Fisherman a couple of those Birds, but he refused, alledging that they served to maintain him and his Family; neither could he inform us whence those Birds came nor how they were first instructed; only he told us, that they were left him by his Ancestors. We asked him likewise whether they ever bred with him; who answered, very rarely. We bought a Dish of Fish of this old Man, which were most of them Carps of a Span and a half long.

Nieuhof's illustration of the fishing cormorant and of the actual fishing, the first portrayal ever made, is reproduced herein as Figure 1 in this article. In the fore-



FIG. 1. The earliest figure of cormorant-fishing ever published (1665). In the foreground is the cormorant, in the middle ground a cormorant-fishing scene, and in the background a typical Chinese landscape.

—After Nieuhof, 1665.

ground is "the bird Louwa" with its hooked beak, its large neck and throat and its palmate feet (very erroneously drawn). In the background is a conventional Chinese landscape. In the middle on the stream is a cormorant-fishing scene. Here are a boat with two roofed-over shelters, three fishermen and four cormorants. The one on the roof has probably been fishing, as it is stretching its wings to dry them. In the water are four birds; one in the left distance, another on the left bringing a fish to its master, on the right one bird is diving and another sitting quietly on the water. At the extreme right is another boat with cormorants.

The boat, fishermen and birds shown in the center are also found in another figure preceding the other in Nieuhof's book—in a view of Suchu (Soochow?) and surroundings. It has seemed best, however, to reproduce the second illustration since it contains a large figure of the cormorant itself as well as a better representation of the fishing scene.

Olfert Dapper,<sup>s</sup> a medical man in the service of the Dutch East India Company, went to China in 1662 in the entourage of Jan van Kampen and Konstantyn Nobel, ambassadors to the emperor of China. His description of China makes up the second part of his great folio published at Amsterdam in 1670. In this he gives us an interesting description and figure of cormorant-fishing. His account so nearly parallels Nieuhof's as to lead one to think that he has for the most part transliterated Nieuhof; at any rate it contains nothing new and need not be given herein.

Dapper's figure, reproduced herein, is such an interesting one as to call for comment. There seems to be little doubt that it was made from actual scenes sketched in

<sup>s</sup> Dapper, Olfert. "Beschryving des Keizzeryks van Taising of Sina," etc., Amsterdam, 1670, pp. 233-235, fig. This is the second part of his "Gedenkwaardig Bedryf Der Nederlandsche Oost-Indische Maetschappye, op de Kuste en in het Keizerrijk van Taising of Sina," etc., Amsterdam, 1670. The German version is "Gedenkwürdige Verriehung der Niederlandischen Ost-Indischen Gesellschaft in dem Kaiserreich Taising oder Sina," etc., Amsterdam, 1675, pp. 141 and 142, fig.



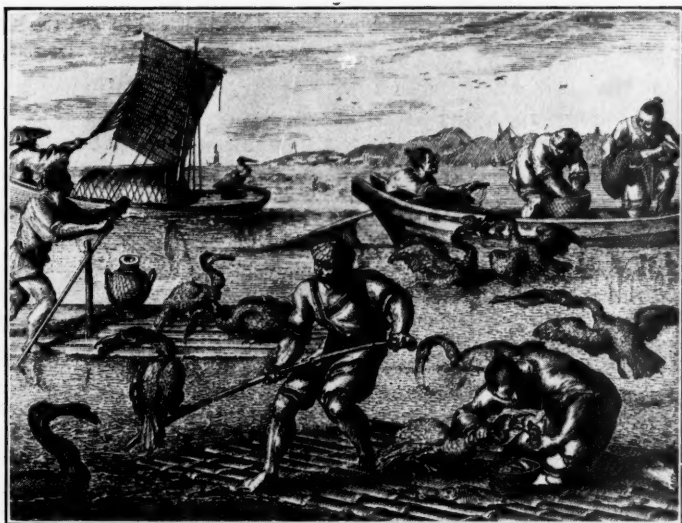


FIG. 2. The second oldest cormorant-fishing figure (1670). All the various activities of these fisherman birds are here portrayed. Note the ligature around the neck of each bird.

—After Dapper, 1670.

China. Here are two rafts of the kind described by Nieuhof and also two boats. On the first raft are two fishermen; one of whom is lifting out on a pole a bird with its catch in its mouth, while nearby is another bird waiting its turn. The other fisherman is holding a cormorant by the throat with his right hand, while in his left is a fish which he has just taken from it. Protruding from the bird's throat into its mouth is seen the tail of another fish. In the basket and on the bamboos composing the raft are found other just caught fishes. The man on the second raft with two cormorants and a water bottle is propelling the raft forward by means of his push-pole.

The boats and their occupants need no particular notice, but in the middle ground (or more correctly water) the actions of the fishing birds call for mention. One bird with open mouth is just striking at a passing fish, another has caught a fish too large to swallow and

holding it by the head, the body in a line with the vertical plane of the head and neck, is flying with it to the boat. Another bird has caught a fish too large for it to bring in and a companion has come to its aid. Each of these birds has a broad ligature around the lower part of the throat but not one has the wings tied together. Certainly this is a charming picture, the second oldest ever published.

Arnoldus Montanus in his "Atlas Chinensis," London, 1671, brings together various data from various authors. He takes freely from Nieuhof the fishing-with-the-cormorant story among others and copies Dapper's illustration. He adds nothing to our knowledge and need not detain us. Reference is made to him to keep our chronology straight and to set forth the above facts.

Navarette<sup>9</sup> was a Catholic missionary in China about the middle of the sixteen hundreds. Among other interesting things which he describes is a fishing scene with cormorants for the chief actors. He tells us that he saw it himself. He writes:

Many of the Chinese bread up Sea-Crows to fish with, and sell them from one Province to another. It is the prettiest pastime in the World, I think, to see the manner of fishing with them. I will write what I saw my self, and observ'd at leisure. Ten or twelve little Boats, at the first dawning of the Sun, appear'd on a spreading and soft flowing part of a mighty River; just as I was sailing that way, I stopt to see the sport. Every boat had four or five Crows at the Head, they were stretching out their Wings, and picking themselves. Being come to the place they design'd, the Boats drew up in a large Ring, and they began with their Oars to make a regular noise; then one or two of the Crows leap'd off from the Boat and div'd, catch'd a Fish, and everyone return'd to his own Boat without ever mistaking, being led by the sound of their Master's Oars. Thus they plung'd into the Water, and return'd to the Boats, which was a great diversion to all that attentively observ'd them. Those that caught large Fishes, brought them in their beaks, and the Fishermen took them in their hands; they that took small Fishes, swallow'd them, and when they were come out of the Water into the Boat, the Men laid hold of them; and holding down their Beak, gave them a gentle stroke on the Neck, whereupon they immediately cast up all the Fishes they had in their Graw. Thus they went on till they fill'd their Baskets with Fish, which was not long a doing, and then they went away up the River to their Homes, carrying the Crows on the Prow as they had

<sup>9</sup> Navarette, Domingo Fernandez. "Tratados Historicas, Politicas, Ethicas y Religiosas de la Monarchia de China," Madrid, 1676. English version in Churchill's "Collection of Voyages and Travels," London, 1704, vol. I, p. 44.

done before. What I admir'd was, that when a Crow had plung'd into the Water, and come up at a great distance from his own Boat, and near another, he immediately went away to his own without regarding the rest.

When they come home, they pick out the smallest Fish, and give them to eat; thus their Masters feed them, and maintain their Families with the large and middle Fish. There is a great deal of difference between seeing and relating it. I must say again, it is one of the prettiest Diversions in the World.

This first-hand account is very charming indeed and it gives us a number of details not found in any of the previous accounts. These are the sailing of the little fleet in the early morning with the birds stretching their wings to catch the warmth of the rising sun, the forming of the boats into a circle, the beating of the water to scare the fishes, the gentle stroking of the neck of the bird to make it disgorge, the coming straight to its own boat of a bird which had emerged at a distance and near another boat—truly all these things make “one of the prettiest Diversions in the World.”

Le Comte (1696), another Jesuit missionary to China, wrote a work on that kingdom which was much reprinted and translated. The *premier* edition is “Nouveaux Mémoires sur l’Etat Present de la Chine” (Paris, 1696, 3 vols.). Fishing with the cormorant is found in Vol. I, pp. 495 and 496. An English version is “Memoirs and Observations . . . Empire of China” (London, 1697). Le Comte’s account differs little from the preceding. He relates that the birds go to the fishing grounds perched on the gunwales of the boats, that one fisherman can manage 100 of them, that on the word being given they fly in all directions, that “they divide amongst them the whole breadth of the River or the Lake; they seek up and down, they dive, and come, and go upon the Water an hundred times, till they have spied their Prey.”

Jean Baptiste Du Halde,<sup>10</sup> a Jesuit missionary in China, published a description of China in four folio vol-

<sup>10</sup> Du Halde, Jean Baptiste. “Description Geographique, Historique, Chronologique, Politique, et Physique de l’Empire de la Chine,” etc., Paris, 1735. Fishing with the cormorant, Vol. II, p. 142; plate to face page 162. Various editions and versions have been published. Englished as “Description of the Empire of China,” etc., London, 1738. Fishing with the cormorant, Vol. I, p. 316; plate to face page 300. An earlier English version, London, 1736, not seen.

umes at Paris in 1735. His account adds little new to our knowledge, but he does say that the fisherman gives the signal to the cormorants by striking the water with an oar, and that when a laden bird comes to the boat "the Fisher-man . . . takes the Bird and holding it head downwards, passes his Hand along the neck to make it disgorge the small Fish it had swallow'd." This turning the bird upside down would certainly expedite the delivery of the fish from the capacious gullet.

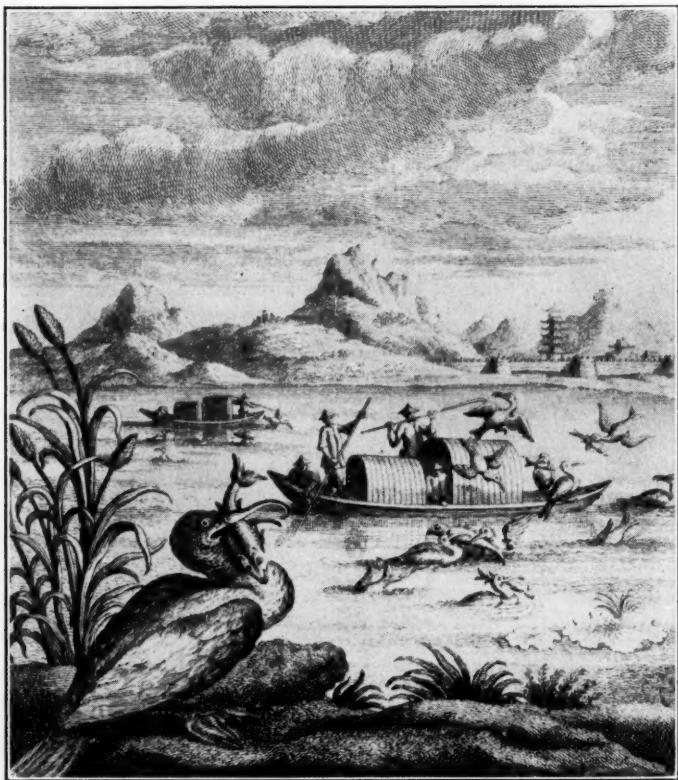


FIG. 3. The third oldest figure of fishing with the cormorant. This is a combination redrawing of figure 1 (Nieuhof, 1665) and figure 2 (Dapper, 1670).

—After Du Halde, 1735.

His figure, the third oldest known, is a composite of Nieuhof's and Dapper's illustrations. The bird in the foreground, the boats and the background are Nieuhof's, but the activities of the birds in the water are from Dapper. Note the two diving birds, another which has just emerged with a fish, two others jointly bringing in a large fish, another flying to the boat with a fish in its beak, while yet another with an air of virtue sits on the gunwale awaiting praise from its master. This is truly a very lively and interesting picture. (See my figure 3.)

The first extended account of cormorant-fishing and the first figure are contained in a work describing the experience of an early embassy to the Chinese empire, and we now come to another and much later one. In the years 1792-1794 Lord MacCartney headed an English embassy to the Middle Kingdom. Two accounts of this were written up by members of the embassy party and both tell us of fishing with the cormorant. The first is from the pen of Æneas Anderson.<sup>11</sup> His naïve narrative indicates that he had never heard of cormorant-fishing before going to China, and he hardly thinks that people will believe him. He adds nothing new and need not detain us longer.

The next account is from the pen of Sir George Staunton,<sup>12</sup> who evidently saw the fishing and who had drawn the figure which is herewith reproduced. His account tells us that on a journey to Han-Choo-Foo in Chekiang:

The Embassy had not proceeded far on the southern branch of the canal when they arrived in the vicinity of the place where the *Leutze*, or famed fishing bird of China, is bred, and instructed in the art and practice of supplying his owner with fish in great abundance.

... On a large lake close to this part of the canal, and to the eastward of it, are thousands of small boats and rafts, built entirely for this species of fishery. On each boat or raft are ten or a dozen birds, which, at a signal from the owner, plunge into the water; and it is astonishing to see the enormous size of fish with which they return, grasped within their bills. They appeared to be so well trained, that it did not require either ring or cord

<sup>11</sup> "A Narrative of the British Embassy to China in the Years 1792-1794," Basil and New York, 1795, p. 277.

<sup>12</sup> Staunton, Sir George. "An authentic Account of the Embassy from the King of Great Britain to the Emperor of China," etc., London, 1797, Vol. II, pp. 338 and 339, fig.

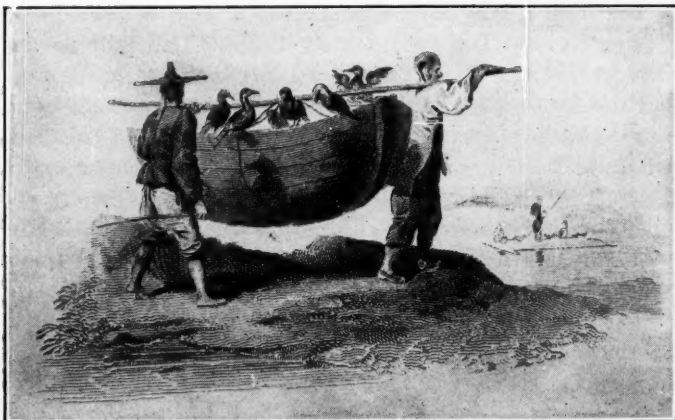


FIG. 4. Sketch showing fishermen carrying their boat and birds to the river. The birds, which have cords attached, sit on the gunwales. On the river is a raft with a fisherman and other cormorants.

—After Staunton, 1797.

about their throats to prevent them from swallowing any portion of their prey, except what the master was pleased to return to them for encouragement and food. The boat used by these fishermen is of a remarkable light make, and is often carried to the lake, as appears in the engraving underneath, together with the fishing birds, by the men who are there to be supported by it.

From 1800 on the accounts of cormorant-fishing in China are literally "too numerous to mention," and only those will be quoted which give us new data or have interesting illustrations. The first of these is Malpière<sup>13</sup> (1825), who gives the interesting figure reproduced herewith, and adds new data as to the method by which the fish is actually caught. He writes:

At a signal given by the master the bands of cormorants, perched on the edge of the wherry or the rafts of bamboos, launch into the water, and follow their prey and seize it with their curved beaks or their palmate feet. The nail [ongle] of the second digit of their feet is denticulate like a saw, which easily enables them to hold a fish with slick scales. If it is too large several go after it and together bring it to the boat. They get on the long oars held out to them, and abandon to their master the first prey to go after a second. . . . The boats employed in this fishery [see annexed figure] are so light that the boatmen sometimes carry them on their shoulders to the margins of the lakes and rivers.

<sup>13</sup> Malpière, D. Bazin de. "La Chine, Mœurs, Usages, Costumes," etc., Paris, 1825, Vol. I, pl. xvii and descriptive text (no pagination). Also 2nd ed., "La Chine et les Chinois," Paris, 1848, Vol. III, pl. xci, and text.



This is the first and I believe the only account in which it is noted that the birds use their feet as well as their beaks for catching fish. Malpière adds the interesting point that if they are well trained they do not need a collar to prevent their swallowing the fish. In this respect they are like our well-trained bird dogs which retrieve birds without ever offering to eat them. The annexed figure shows the birds without the collar.



FIG. 5. De Malpière's figure (1825) of fishermen, boat and cormorants.

The second account *post* 1800 is from the pen of a man who in his day and generation had an unsurpassed knowledge of things Chinese. S. Wells Williams<sup>14</sup> tells us that "the fishing cormorant of China (*Phalacrocorax sinensis*) is called [by the Chinese] *loo-sze*, the etymology of which is 'the black [bird] in the reeds,' another name is the 'old water crow,' which is similar to the French name *corbeau marin*, from whence comes our English

<sup>14</sup> Williams, S. Wells. "The Loo-sze or Fishing Cormorant." Selected from Chinese Authors. The Chinese Repository. Canton, 1839, vol. 7, pp. 541-543. This account is also to be found in the various editions of his work. "The Middle Kingdom," New York and London, 1848, and many later editions.



FIG. 6. A cormorant fetching a fish to its master. Another is perched falcon-fashion on the wrist of its owner.

—After Allom and Wright, 1843.

word cormorant; 'the black devil' is an appellation given to it by fishermen . . . In the poems of Toopoo is this couplet:

"Every family trains the black devil,  
Which, after diving, seizes the yellow fish;"<sup>15</sup>

Allom and Wright<sup>16</sup> give a beautiful steel engraving (see the annexed figure) of fishing with the cormorant.

<sup>15</sup> With regard to the couplet from Toopoo or Tu Fu, Dr. Laufer informs me that many Chinese scholars have doubts as to whether this refers to the cormorant. Personally, he does not think that it does.

<sup>16</sup> Allom, Thomas, and Wright, G. N. "China, in a Series of Views . . . by Thomas Allom . . . Descriptive Notices by G. N. Wright," London, 1843, Vol. II, p. 66, pl.

Here one sees in Allom's drawing a cormorant with a large fish in its beak swimming towards the boat and to its master, who with outstretched hand waits to receive it. Another fisherman has another cormorant perched falcon-like on his wrist. Wright's remark on the training of these birds is worth quoting if only for its absurdity: "In this most tedious process [of training], the sagacity of the cormorant is alone entitled to our admiration; the indefatigable patience, that caused its development, deserving little more than our compassion."

Father Ripa, in his "Memoirs during Thirteen Years Residence at the Court of Peking" (London, 1844, p. 40), gives us one new point. He says that when the fisherman perceives that the bird has a full gullet and moves with difficulty, he holds out to it his pole. The bird climbs onto this and is helped into the boat. This, however, is shown in Dapper's figure on p. 15 and was evidently an old practice, but one first specifically noted by Ripa.

Fortune (1847),<sup>17</sup> a skilful observer, gives some interesting points worthy of quotation. Among other things, he says that near Ningpo:

There were two small boats, containing one man and about ten or twelve birds in each. The birds were standing perched on the sides of the little boat, and apparently had just arrived at the fishing ground, and were about to commence operations. They were now ordered out of the boats by their masters; and so well trained were they, that they went on the water immediately, scattered themselves over the canal, and began to look for fish. They have a beautiful sea-green eye, and, quick as lightning, they see and dive upon the finny tribe, which, once caught in the sharp-notched bill of the bird, never by any possibility can escape. The cormorant now rises to the surface with the fish in his bill, and the moment he is seen by the Chinaman he is called back to the boat. As docile as a dog, he swims after his master, and allows himself to be pulled into the Sanpan, where he disgorges his prey, and again resumes his labours. . . . Sometimes a bird seemed to get lazy or playful, and swam about without attending to his business; and then the Chinaman, with a long bamboo, which he also used for propelling the boat, struck the water near where the bird was, without, however, hurting him, calling out to him at the same time in an angry tone. Immediately, like the truant school-boy who neglects his lessons and is found out, the cormorant gives up his play and resumes his labours.

<sup>17</sup> Fortune, Robert. "Ten Years' Wanderings in the Northern Provinces of China," 2nd ed., London, 1847, pp. 98 to 103. Also, "Two Visits to the Tea Countries of China," 3rd ed., London, 1853, Vol. I, pp. 86 to 90.

Fortune was very anxious to procure specimens to take home to England. These, after much trouble, he obtained, through the help of the English consul at Shanghai, from a professional breeder of fishing cormorants, but his troubles had only begun. He relates further:

The difficulty now was to provide food for them on the voyage from Shanghai to Hong-kong. We procured a large quantity of live eels, this being a principal part of their food, and put them into a jar of mud and fresh water. These they ate in a most voracious manner, swallowing them whole and in many instances vomiting them afterwards. If one bird was unlucky enough to vomit his eel, he was fortunate indeed if he caught it again, for another, as voracious as himself, would instantly seize it, and swallow it in a moment. Often they would fight stoutly for the fish, and then it either became the property of one, or, as often happened, their sharp bills divided the prey, and each ran off and devoured the half which fell to his share. During the passage down we encountered a heavy gale at sea, and as the vessel was one of those small clipper schooners, she pitched and rolled very much, shipping seas from bow to stern, which set everything on her decks swimming. I put my head out of the cabin-door when the gale was at its height, and the first thing I saw was the cormorants devouring the eels, which were floating all over the decks. I then knew that the jar must have been turned over or smashed to pieces, and that of course all the eels which escaped the bills of the cormorants were now swimming in the ocean. After this I was obliged to feed them upon anything on board which I could find; but when I arrived at Hong-kong, they were not in very good condition; two of them died soon after; and as there was no hope of taking the others home alive, I was obliged to kill them and preserve their skins.

It has probably occurred to the reader to query whether or not this cormorant will breed in captivity, whether the eggs can be hatched and the young reared and trained.<sup>18</sup> Fortune went pretty fully into the matter and we will let him answer the question, since he seems to be the first recorder of the process.

The Chinaman from whom I bought these birds has a large establishment for fishing and breeding the birds about thirty or forty miles from Shanghai, and between that town and Chapoo. They sell at a high price even amongst the Chinese themselves—I believe from six to eight dollars per pair, that is, from 30s to 40s: As I was anxious to learn something of their food and

<sup>18</sup> I had thought of putting as a finale to this article a section describing the method of training the young cormorants to fish, but learning that Dr. Berthold Laufer is interested in the ethnological aspects of this question of the domestication of the cormorant, it seems best to leave this specific subject for his able hand. However, since all reference to the training of the young can not be omitted herein without serious detriment to this article, the data on training the young will simply be given *pari passu*, leaving special consideration of the subject to Dr. Laufer.

habits, Mr. Medhurst, Jr., interpreter to the British Consulate at Shanghai, kindly undertook to put some questions to the man who brought them, and sent me the following notes connected with this subject:—

The fish-catching birds eat small fish, yellow eels, and pulse-jelly. At five P. M. every day each bird will eat six taels (eight ounces) of eels or fish, and a catty of pulse-jelley. They lay eggs after three years, and in the fourth or fifth month. Hens are used to incubate the eggs. When about to lay their faces turn red, and then a good hen must be prepared. The date must be clearly written upon the shells of the eggs laid, and they will hatch in twenty-five days. When hatched, take the young and put them upon cotton, spread upon some warm water, and feed them with eels' blood for five days. After five days they can be fed with eels' flesh chopped fine, and great care must be taken in watching them.

When fishing, a straw tie must be put upon their necks, to prevent them from swallowing the fish when they catch them. In the eighth or ninth month of the year they will daily descend into the water at ten o'clock in the morning, and catch fish until five in the afternoon, when they will come on shore. They will continue to go on in this way until the third month, after which time they cannot fish until the eighth month comes round again. The male is easily known from the female, in being generally a larger bird, and in having a darker and more glossy feather, but more particularly in the size of the head, the head of the male being large and that of the female small.

Such are the habits of this extraordinary bird. As the months named in the note just quoted refer to the Chinese calendar, it follows that these birds do not fish in the summer months, but commence in autumn, about October, and end about May—periods agreeing nearly with the eighth and third months of the Chinese year.

It has been alleged by Fortune that the cormorants are not used for fishing during the summer in the neighborhood of Shanghai, but Milne<sup>19</sup> on July 14 saw them so used in the department of Kinhoa, on the river Toungyang, at the foot of the rapid called Toun-gtsze-chan. There were two men and a score of cormorants in a small boat. The birds were under perfect control and wore no strap or ligature around their necks. The fishing, however, was always done when they were fasting.

Huc<sup>20</sup> saw this fishing carried on on the river Ping-hou, and adds two details not noted by any previous writer. Indeed, the method noted of the double tying of the fisherman bird is not reported by any one else from China,

<sup>19</sup> Milne, William C. "Life in China," London, 1857, p. 307.—"La Vie Réelle en Chine" (Fr. version by A. Tosset). Paris, 1858, pp. 296-297.

<sup>20</sup> Huc, ———. "The Chinese Empire," etc., London, new ed., 1859, pp. 334-335.

nor has any one else noted that the birds pair off on either gunwale to preserve the equilibrium of the boat. Hue says:

... to prevent their straying about in the water and wasting the time destined for work, a cord is attached to the ring and to one claw of the cormorant, by which he is pulled up when inclined to stay too long under water. . . . In passing from one fishing ground to another, the cormorants perch side by side on the edge of the boat, and their instinct teaches them to range themselves of their own accord in nearly equal numbers on each side, so as not to disturb the equilibrium of the frail vessel; we saw them thus ranged throughout the little fleet of fishing smacks on Lake Ping-hou.

Frauenfeld<sup>21</sup> in the same year (1859) noted some interesting details in the management of birds seen at the town of Tsing near Shanghai. The fisherman standing in the rear of the boat lifted the cormorants into the water by means of a bamboo pole. "By a kind of short cry accompanied by rhythmic stamping of his feet, and by striking the water with his pole, he directed the birds, incited them to dive, and meanwhile pushed his boat forward." Asked to put a price on one of his birds, he asked 12 000 *cash* or about \$8.

John Scarth in his "Twelve Years in China," Edinburgh, 1860 (pp. 42-43), often saw this fishing carried on, but it was best visible in the clear waters of Chekiang. He writes that "It is very pretty to see the birds chasing the fish under the water—the pace they go at is wonderful; and when they are swimming along near a rough stony bottom, it is quite marvellous to see the rapidity with which they crane their necks from side to side in the crevices of the rocks as they rush through the water." He thinks that rings are placed around their necks not so much to prevent the swallowing of fish as to distinguish the birds belonging to each fisherman. This he thought because in a fishing company each lot of birds had a different mark.

Justus Doolittle<sup>22</sup> observed at Fuhchau an entirely new method of landing a cormorant which has captured a large fish. In case a bird caught a fish too large for it

<sup>21</sup> Frauenfeld, ———. "Notizen über die Faune Hongkong's und Schanghai's" [while on the "Novara" in 1858]. *Sitzungsberichte Akademie Wissenschaften Wien*, 1859 (Math.-Natur.-Klasse), vol. 35, p. 257,

<sup>22</sup> "Social Life of the Chinese," New York, 1865, Vol. I. pp. 55-57.





FIG. 7. Doolittle's figure (1865) of a fisherman on a bamboo raft ready to retrieve both fish and bird with a dip net.

successfully to bring in by itself, the early writers allege that a second would also lay hold and help. In fact, Dapper shows this in his figure on page 15. Doolittle says that this often occurs, but that "sometimes the fish is a large one, and there is evidently a struggle between it and the cormorant. The fisherman, when near enough, dexterously passes a net-like bag, fastened to the end of a pole, over the two, and draws them both on the raft"—as is indicated in his figure reproduced herewith. Some-

times two birds would quarrel for the fish one had taken, or one bird would chase another.

Dabry de Thiersant (1872)<sup>23</sup> begins his exhaustive work on the fisheries of China with the following words: "The Chinese have brought the art of fishing to a very high degree of perfection. They have known how to utilize everything that nature has put at their service to find and take fishes in the depths or at the surface of the water." He then proceeds to justify this statement by portraying, in thirty-five folio plates and 118 figures with



FIG. 8. A Chinese drawing of a cormorant-fishing scene. "The bateaux employed . . . are very light, and each is three feet long by one and one-half wide. Two of these wherries are united by two planks on which the fisherman stands. The young cormorant has just caught a fish.

—After Dabry de Thiersant, 1872.

<sup>23</sup> Dabry de Thiersant, P. "La Pisciculture et la Pêche en Chine," Paris, 1872, pp. 171 to 173, pl. xix, fig. 1.

accompanying explanations of their working, these many and vastly ingenious fishing implements. These figures seem to have been drawn by Chinese artists presumably under his direction.

However, we are here mainly interested in what Dabry de Thiersant has to say about cormorants, which he avers are very much esteemed as fishermen, especially in the provinces of Hou-nan and Ho-nan. Moreover, what he writes, coming apparently at first hand, with regard to the manner of breeding and training cormorants is of especial value and will be quoted in full and his figure reproduced. This full account should be contrasted with the shorter one given by Fortune on page 25.

The cormorants ought to lay at two years and at the moment of this act, which generally takes place in the third quarter of the moon, when they prepare in a spot retired and obscure a nest of straw, on which the female comes to lay her eggs, which she herself covers all the time. The incubation lasts thirty days. During the first seven days they give to the young birds meat chopped very fine, which is placed before them three times a day and which they prefer to all other food. However, after this time, little fishes are added to the ration of beef meat. On the tenth day the trainer takes the little cormorants on his *bateau* (pl. xix, fig. 1) when they seek their places on the common perch, the wood of which is covered with hemp. As soon as they are strong enough they are put in the water and allowed to stay for some minutes in the midst of their elders. At the end of some weeks, they are already marvellously trained to catch and retain in transit little fishes which are thrown them from the boat. It is only after seven or eight months that they are well enough trained for fishing.

There is then placed on the neck of each a collar of *teng-tse* (rattan) to prevent the swallowing of the fish. To the foot of each is fastened a small cord, about two feet long, and attached at the other end is a float of bamboo or wood. On a signal being given by the fisher, who stands on his *bateau* with his hand armed with a forked pole five or six feet long, all the cormorants plunge into the water, seek for their prey, and, when they have seized it, come to the surface each holding a fish in his beak. The fisherman then hooks the float with his long pole, on which the cormorant now mounts, and with his hand takes the fish which is thrown into the net. When the fish is very large and heavy, i.e. of seven or eight pounds, the cormorants offer mutual assistance; one takes the fish by the fins, another by the tail, etc.

If the birds are lazy and will not fish, the fisherman pushes them off his boat with his pole and even taps them on the head with it. On the other hand, they are usually given two hours' rest in the middle of the day. According to this authority, cormorant fishing is carried on



FIG. 9. Native sketch of a cormorant-fishing scene on a mountain river in Kwang-tung.

—After Gray, 1878.

throughout the year even in the dead of winter, unless interrupted by the freezing of the streams. The birds are serviceable up to the age of ten years, and much care is given them—for instance, they are dosed with oil of sesame if they get sick. When the fishermen go out to fish in companies, each man has his birds marked with his own mark.

According to Garnier<sup>24</sup> (1873) the fishermen on Lake Taly, the source of the Mekong River, near Too-ton-tse town in the province of Yunnan, have devised a most ingenious method of increasing the efficiency of their cormorants. Early in the morning, accompanied by their birds, they embark in their boats and let these drift with the wind and current while one man standing in the prow casts large pellets of rice on to the surface of the water. The fishes launch themselves at this food in great numbers and the cormorants launch themselves at the fishes with the usual results, and very shortly the boat is loaded and on its way to market.

<sup>24</sup> Garnier, François. "Voyage d'Exploration en Indo-Chine," etc., Paris, 1873, Vol. I, pp. 517 and 518. This particular account is also found on page 129 of an anonymous work, "The French in Indo-China," London, 1884.

Throughout eastern China generally and particularly along the Grand Canal, Gray<sup>25</sup> (1878) saw cormorants everywhere utilized for fishing. Rafts or catamarans were used in a mountain river in Kwang-tung (see his figure, apparently drawn by a native artist, herein reproduced). On the Poyang Lake rather large boats were used with special roosts running along the sides of the boats fore and aft for the birds to perch on. Here also the fisherman used a hand-net to receive the fish while the bird was still in the water. One paragraph of this account is sufficiently interesting to warrant inclusion in full:

At Hang-chow, a prefectural city at the southern extremity of the Grand Canal, I saw not less than five-hundred cormorants engaged in fishing at one time, and within a space of one-eighth of a mile. Many of the birds were young and imperfectly trained; and when it happened that one of them caught a fish, he was instantly pursued by a great many other cormorants, each bent upon robbing him of his prize. A scene of great confusion and excitement was the result of this undisciplined behaviour. It was interesting to observe the ease with which, in the midst of the disorder, each fisherman recognized his own birds. The boats they used differed from those which I have described elsewhere, being very light, and in shape not unlike canoes.

Colquhoun<sup>26</sup> (1883) figures (*from an original sketch*) cormorants sitting on curious perches at one end of the boats used on the Si-kiang or West River near Nga-paw and Pe-sê. However, in his text (where the account is very brief) he speaks of their sitting on the gunwales. On the West River, long nets were used "forming channels into which the fish are driven," making it easier for the birds to get the fish. It would seem that seated on such elevated perches the birds would not only have a more extended range of vision but would be able to see fishes nearer at hand but deeper in the water.

Jametel<sup>27</sup> (1886) gives a long and interesting account of the hatching, rearing and training of fishing cormor-

<sup>25</sup> Gray, John Henry. "China: a History of the Laws, Manners, and Customs of the People," London, 1878, Vol. II, pp. 297 and 298, pl.

<sup>26</sup> Colquhoun, Archibald R. "Across Chryse, being the Narrative of a Journey . . . from Canton to Mandalay," 3rd ed., London, 1883, Vol. I, pp. 233 to 235, fig.

<sup>27</sup> Jametel, Maurice. "La Chine Inconnue," Paris, 1886, 3rd ed., pp. 208 to 213.



FIG. 10. Cormorant-fishers on the West River.

—After Colquhoun, 1883.

ants. However, only one or two points will be noted wherein his account supplements or differs from those previously given. Rearing is extensively carried on in the province of Tche-kian. The first eggs are laid generally in February, but are placed under hens for hatching since the female cormorants care very little for maternal duties. The young ones come out of their shells, after a month of incubation, so feeble that they can not stand on their feet and susceptible to cold to such an extent that the least drop in temperature would kill them. For this reason, right after their birth, they are placed in baskets lined with cotton and kept at a relatively high temperature by means of artificial heat. They are fed pills made of a mixture of peas and eel meat chopped fine or ground up. After about a month they begin to have a fair coat of feathers. From this time their feeding and education go on simultaneously. Jametel's description of this is as follows:

As soon as the young cormorants have attained their growth, that is about five months after their birth, there is attached to the foot of each a string,



the other end of which is fastened to a stake set in the bank of the stream or pond. The trainer then pushes them into the water with a pole, all the time whistling an air which for the young birds is the signal for "launching into the water." The trainer then throws to them some little fishes on which they pounce with all the more voracity since throughout all the time of their training, they have been given very little food. Then their trainer whistles another air, which is for the cormorants the signal of "retreat," and, in order to make them understand, at the same time he twitches the cord which is attached to their feet and thus forces them to return to land. After two or three months of such lessons repeated several times every day, they begin to be trained on a boat in the same manner as on land, and it is not until after another period of a month's training on a boat that the young cormorants are able to fish without the help of the cord. However, there are found among cormorants, as among men, some who are more or less gifted. Thus there are those who know how to fish well before the two months of training are ended, while, on the contrary, there are those incapable of fishing even after this period and are condemned to finish their existence in the soup pot of their trainer. Those who have finished their education are generally valued at 30-35 francs each if they are males, the females always being of less price because she is weaker and consequently fishes more slowly.

At the end of about their fourth year, the birds begin to show their age by a gradual loss of plumage, and they almost all die by the end of the sixth year.

In the *East of Asia Magazine* for 1903 (Vol. 2, pp. 95-97), there is an anonymous article, entitled "Cormorant Fishing," with four illustrations made from photographs. The account is the usual stereotyped one and hence is inconsequential. The figures show the fishermen and their boats with the birds perched on their gunwales or swimming in the water—none show actual fishing, and none are worth reproducing here. The article is noted here that the reader may not be misled as to its value by the definite title.

In "The Romance of the World's Fisheries," by Sidney Wright (London, 1908), there is on pages 182 to 185 an interesting account of cormorant-fishing in China. There is little, however, that is new, and since the new things (however probable) are unsupported by references, one can but suspect that they are *written in* to make the story read more smoothly and interestingly. It does not seem worth while to quote them here.

Gordon Moir has an interesting article "Some methods of fishing in China," in the *Badminton Magazine*

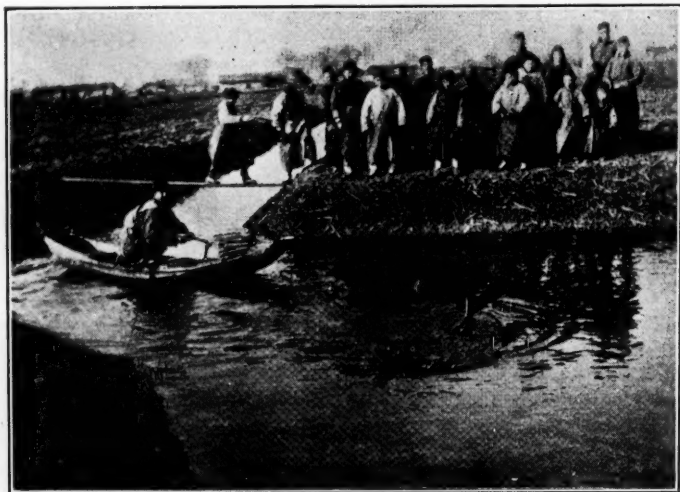


FIG. 11. Cormorant-fishing in a canal in the level country of southeastern China.

—After Moir, 1909.

(1909, Vol. 29, pp. 279 to 289), illustrated by photographs. His three figures of cormorant fishing show the boats with fishermen and birds in different positions, but only one portrays an actual fishing scene. This figure is here-with reproduced. From that part of his account dealing with these birds the following excerpts are taken, the first paragraph having to do with the training, the others with the fishing proper.

The sampan is very small, containing the fisherman and about six or seven birds. The Chinaman has a bamboo in his hand, and the birds, which are resting on projections on either side of the boat, are pushed overboard, when they immediately dive. The fisherman then rocks the sampan from side to side, presumably to make the birds keep away and spread themselves. A cormorant soon arrives on the surface with its catch, and tries to swallow the fish. The bamboo pole is thrust towards it, the bird perches on it, and it is brought on board still trying to complete its meal. The fish is removed, and the bird sent overboard again. At the end of the third or fourth journey the band is removed from the cormorant's throat, and it is given a small piece of one of the fish to eat. . . .

A fleet of these craft consists of a number of parent sampans large enough to carry four or five very small sampans on their decks. From forty to a hundred cormorants, divided into different sections, are carried in each parent boat.

The small sampans are made just large enough to hold a Chinese boy. They have perches fitted round them supporting short branches where the cormorants can perch. The crew of the parent sampan includes enough boys to man all the small boats, and as soon as the fishing begins, the boys get into their sampans, taking with them the cormorants, which they remove by means of a bamboo. In order to identify the birds each one is marked either by turning or colouring certain wing feathers, so that when the fishing fleet is in company each crew has no difficulty in recovering its own.

When the small sampans have left the mother boat they spread out, and the fishing is carried on from them in the method employed for training the birds, the rocking movement being kept up all the time to make the birds spread. The birds dive in various directions, and a keen eye has to be kept for the reappearance of each one. As one is seen to come to the surface out goes the bamboo, the bird perches on it, is drawn to the boat, the fish removed, and the cormorant is sent overboard again to resume its task.

The next and last quotation comes out of its chronological order, but it seems well to put it here as the closing account in this article since it is an official description bearing the imprimatur of the Chinese government as to the rearing, training, using and caring for the fishing cormorant. It was first published in the "Special Catalogue of the Ningpo Collection of Exhibits," (International Fishery Exhibition, Berlin, 1880), and in *Ibis* (1880, 4th series, Vol. IV, pp. 375 and 376). Later it was published in the "Special Catalogue of the Chinese Collection" at the great International Fisheries Exhibition (London, 1883). Illustrative of this latter account daily exhibitions of cormorants at work were given at London, constituting one of the chief attractions of the exhibition. This collection of cormorants is said to have been purchased by the then Prince of Wales, but I have been unable to trace their history further. The official account of this fishery is as follows:

Many are the ways used in this province [Chehkiang] for catching fish of all kinds in the rivers, lakes, and canals, but none of them are more curious than the cormorant fishing, which may be seen everywhere about Ningpo. Certain places are noted for the excellence of the birds which are bred and trained there; amongst these we may name Fenghua and Shaohsing.

The most celebrated place, however, is a small town called T'anghsichen, 50 li northwest of Hangchow, the people of which are currently believed to possess a secret in cormorant rearing which gives them special success.

The cormorant's book name is *Lu-tzu*, and the common name is *Yu-ying*, or *Yu-ya*, "fish crow."

The females lay yearly from three to nine eggs, in the first and eighth moon. The colour of the eggs is green, but it is much covered with white chalk; their size is that of duck's eggs. The white inside is slightly green, and the eggs are never eaten, on account of their strong flavour.

The eggs of the first season (first moon) are the only ones retained for hatching. Towards the beginning of the second moon, they are given to the hens to hatch, as the female cormorant is a careless mother. The young break their shell after a month's incubation. When new born they can not stand on their legs, and are very sensitive to cold. They are therefore taken away from the hen, placed in baskets filled with cotton wool, and kept in a warm place. The eggs of the second season are not used, the weather being too cold; they are given away to children and beggars.

The young birds are at first fed with a mixture, in equal parts, of bean curd and raw eel's flesh cut fine. If the eels are not procurable, the flesh of the *Hei-yu* (*Ophiocephalus niger*) is used instead, in the form of small pills. At the end of a month the down begins to be covered by the larger feathers, and the quantity of fish-flesh fed to them is increased, while that of bean curd is reduced. A second month elapses, and the young birds, having grown to double their original size, are fit for the market; a male fetches one or two dollars, and a female half as much.

The birds are now fed with young fish thrown to them. When they have attained their full size, a string is tied to one leg, the other end of it being fastened to the bank of a pond or canal. They are then made to go into the water, the trainer whistling a peculiar call and using a bamboo to force them. Small fish are thrown them, upon which they pounce greedily, as they have been kept on short allowance of food. They are now called back by a different whistle-call, and forced to obey by means of the string; as they reach the shore, more fish is given them. This teaching having been gone through daily for a month, another four or five weeks are spent in training the birds from a boat; at the end of this period the string is generally dispensed with. When old and well trained cormorants are made to accompany the young ones, the time required in training is reduced one-half. Birds not properly trained after all the trouble thus taken are pronounced stupid and not fit for use.

The teaching being completed, the cormorants are fed sparingly every morning with fish. A small ring of hemp is tied around their necks to prevent them from swallowing large fish, and they are taken on board the small punt, called "cormorant boat" to the number of ten or twelve. They are now as docile as dogs, and sit perched on the side of the boat until they are sent into the water by a mere whistle from their master. They dive after fish, and bring their prizes to the boat, firmly held in their hooked beaks. When a fish is too large for one bird, three or more join their forces and capture it together. Sometimes the fisherman signals them to dive by striking the water with a long bamboo. If any cormorant is inclined to be disobedient, his legs are connected by a short piece of string; this forms a loop, by means of which the bird may at any moment be brought on board *volens volens* with a long bamboo hook.

After fishing two or three hours, the birds are allowed to come on board and rest. At the end of the day the hempen ring is loosened or removed altogether, and they are either allowed to fish for themselves, or are fed by the hand of their master. Seizing the birds one after another by the upper

mandible, the fisherman thrusts into their throats a handful of small fish and a ball of bean curd, as large as his fist, the ingurgitation of which he helps with the other hand by stroking the neck of the bird, who seems to enjoy it, as he promptly returns for a second supply. The entire scene is most ludicrous. At night the birds are brought home and caged. A cormorant holds out for five years, at the end of which time these birds lose their feathers, and soon after die. The females, being weaker than the males, only catch small fish—hence their lower value. Very good birds reach a value of 10 taels a pair, a well-trained male being worth six or seven dollars. The females lay when one year old.

I now am permitted to reproduce two photographs taken by Dr. C. K. Edmunds, provost of the Johns Hopkins University. Dr. Edmunds was in China from 1903 to 1919 as professor of physics and (for nine years) as president of Canton Christian College. As observer in charge for China and Mongolia for the Department of Terrestrial Magnetism of the Carnegie Institution of Washington, he traveled in every province of China. He found fishing with the cormorant everywhere practiced on the lower sections of the Grand Canal and the con-



FIG. 12. A fleet of cormorant-fishers on the West River.

—Photograph by Dr. C. K. Edmunds, 1907.



FIG. 13. An illustration showing in greater detail an outfit of cormorant-fishers on the West River.

—Photograph by Dr. C. K. Edmunds, 1907.

necting canals in the Yang-tse delta and throughout South China generally. The photographs were taken by him on the Fu River, a tributary of the Si-kiang or West River, in the province of Kwong-si in November, 1907.

The first figure shows six groups of fishermen on their bamboo rafts with their cormorants for catching and their baskets for receiving fishes. They seem to be on their way to the fishing grounds or maybe are returning from these. The rafts sit low in the water—almost awash—with the cormorants mainly at their ends. The second figure gives a nearer view of rafts, baskets, fishermen, and fishermen birds. Dr. Edmunds adds that: "Very often the fishermen have a board on their raft,





FIG. 14. Photograph by Dr. Camillo Schneider of a cormorant-fisherman, boat, and birds, taken in western Yunnan in 1914.

—Copyrighted photograph reproduced by courtesy of the National Geographic Magazine.

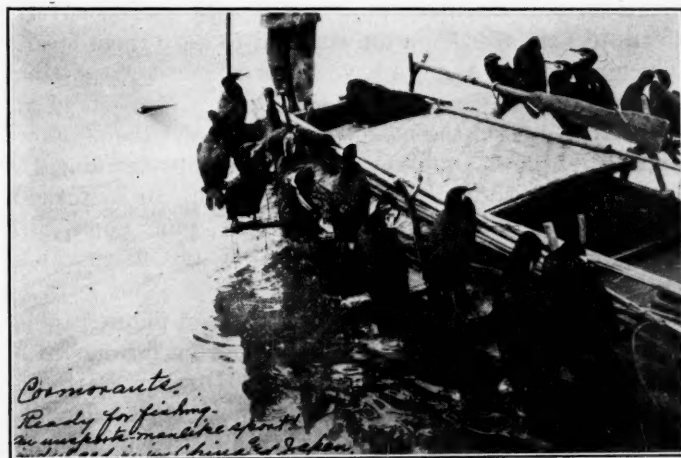


FIG. 15. Photograph taken in 1921 by Mrs. Mary G. Lucas of cormorants ready for fishing on a stream outside of Peking. The cormorants sit on perches extending out at right angles from the boat. In the boat is a "well" provided with a sliding cover to keep the fish fresh.

—Copyrighted photograph reproduced by courtesy of the National Geographic Magazine.

and on this they stamp somewhat rhythmically either with a view to attracting the fish or to stimulate activity on the part of the birds—for apparently the latter are influenced by the sound and bob up and down in unison therewith—but I may have been deceived as to this.”

Finally, I have pleasure in presenting two comparatively recent photographs of cormorant-fishing in China wherewith to complete this article. These are reproduced from the *National Geographic Magazine* through the courtesy of Mr. John Oliver La Gorce, associate editor.

The first was taken by Dr. Camillo Schneider in Western Yunnan in the fall of 1914. Here we have the fishermen in a light boat much like those figured by Gray and by Moir. The cormorants sit on the upturned baskets or on the gunwales. In the middle ground is a rice field, in the background the mountains. The other and last scene was photographed by Mrs. Mary G. Lucas on a small stream a few miles outside of Peking. This gives in admirable fashion the details of the fishing boat. Here there is apparently a “well” with sliding covers to protect the fish from the sun and to keep them fresh. The birds, which seem to have cords attached, are sitting on the sides of the boat or on perches which extend at right angles from the boat (probably to get the cormorants out of the way and certainly to promote cleanliness). Lying on the sliding covers of the “well” or in forked supports set in the gunwales are oars, punt poles, dip nets and the other paraphernalia of the fisherman’s trade.

Lastly I conclude this article by giving a photographic representation of two models of cormorant-fishing rafts which were obtained at Ningpo in 1901 by Dr. Berthold Laufer, who was at that time a member of the department of anthropology in the American Museum. Each of these models consists of a raft made up of six bamboos with upturned forward ends to make propulsion easier; each has a fisherman with his staff, the one bareheaded,

the other with a broad brimmed hat for keeping off sun and rain, and what is apparently a rain coat; each has a receptacle for fishes, one apparently a basket, the other a tub filled with fishes; and lastly each raft carries five cormorants, the attitude of the birds of each set being remarkably alike, but quite different from that of the birds on the other raft. Truly these models make a charming picture.

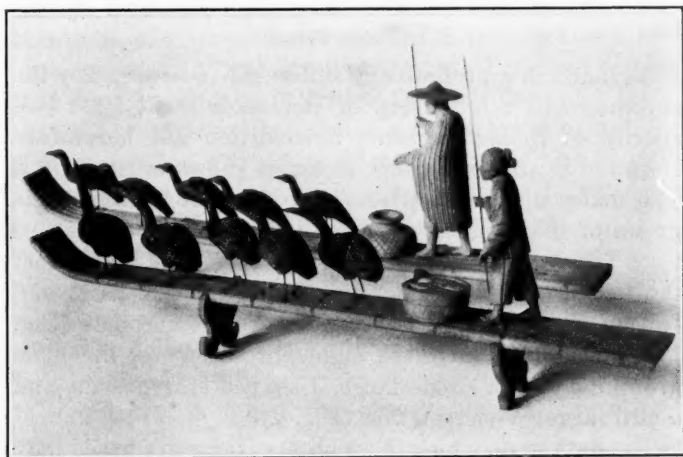


FIG. 16. Photograph of two models in the American Museum of cormorant-fishing craft and fishermen both human and avian. Models collected in Ningpo in 1901 by Dr. Berthold Laufer.

## CHROMOSOME STUDIES ON SCIARA (DIPTERA)

### I. DIFFERENCES BETWEEN THE CHROMOSOMES OF THE TWO SEXES

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#### INTRODUCTION

As noted in a preliminary statement (*Science*, '25) the chromosomal relationship of the sexes in at least two species of *Sciara* presents a condition not heretofore observed in any organisms, so far as known to the writer. The males appear to possess the complete chromosome group of the females, plus two larger chromosomes distinct from all the others. In the species studied most the female group includes two short, rod-like pairs and two medium sized V-shaped pairs of chromosomes (Fig. 1). In addition to these eight chromosomes, the male group includes a single large, J-shaped chromosome and a still larger V-shaped one (Fig. 2).<sup>1</sup>

The data upon which these observations are based may now be given in detail. They include the study of laboratory stocks and of offspring from wild females in *Sciara similans* Joh.,<sup>2</sup> *S. pauciseta* Felt and *S. prolifica* Felt. The species determinations have very kindly been made by Professor O. A. Johannsen.

In the preliminary statement mentioned above several features concerning the chromosomes of *Sciara* were noted in addition to that differentiating the sexes. The present paper, however, will not attempt to deal with

<sup>1</sup> These distinctions, as to shape, are based on the mode of spindle fiber attachment in metaphase, and are, of course, not always clear in the figures, many of which are from slightly earlier or later stages than that which shows the attachment best.

<sup>2</sup> A description of this species, by Professor Johannsen, is in press.

these, since the cytological study is not yet completed and certain peculiarities of chromosome behavior are not yet understood. It will be concerned only with the relationship between the chromosomes of the two sexes, this being an essential preliminary to further work on the maturation phenomena, genetic behavior, etc., in these flies.

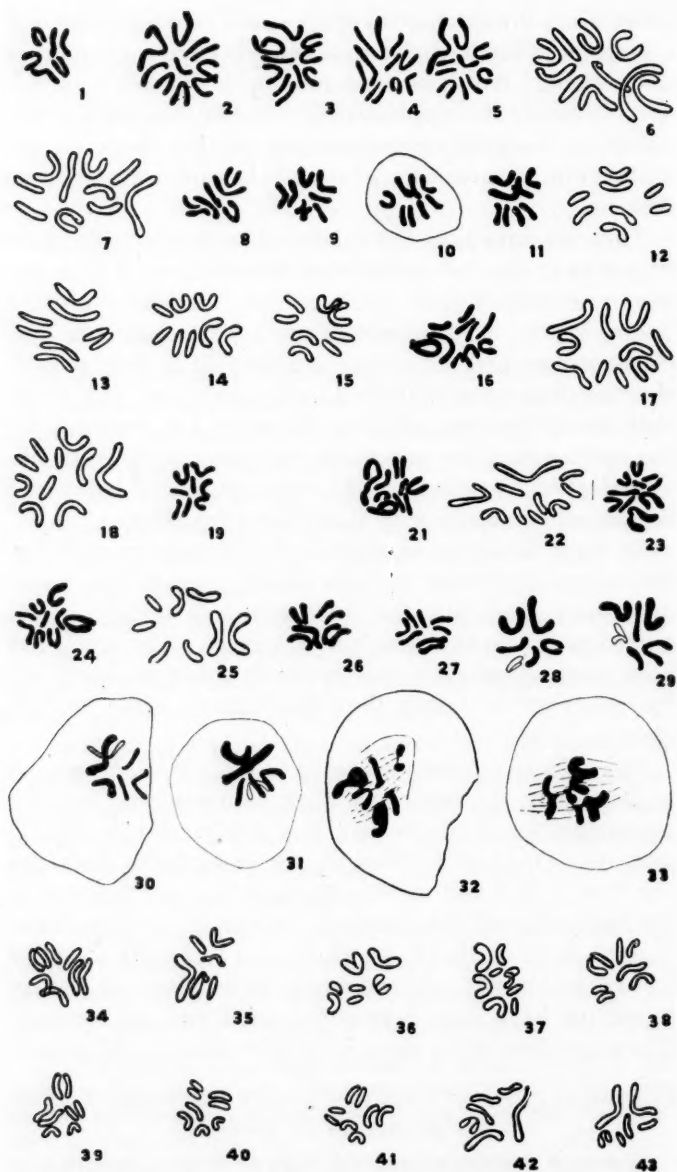
To make sure that the relationship between the chromosomes of the two sexes is as stated above it is necessary to establish three points: First, that the two extra bodies in the chromosome group of the male are real chromosomes and not simply chromatoid bodies; second, that they are actually limited to the male line; and, third, that the differences between the sexes are constant for the species and are not accidental peculiarities of individual stocks or races. The data presented below are concerned primarily with these three features.

To treat the three separately would require considerable repetition, hence the data will be presented as seems most convenient and the discussion will largely be reserved to follow the descriptive portion. The study has been confined mainly to *Sciara similans* and except where the contrary is noted the observations refer to this species.

The writer is greatly indebted to Miss M. S. Moses for assistance in the laborious work of dissecting, and for preparing the slides used in this study. He is also indebted to Dr. José F. Nonidez for making the drawings for Figs. 2 to 5 and to Miss Rachael Haynes for making the remainder of the drawings, except the outline drawings (6, 7, 12 to 15, 17, 18, 22, 25 and 34 to 43) which he has made himself. It should be noted that the figures in outline have been drawn free-hand and not to scale. The magnification in these is greater than in the others.

#### COMPARISON OF THE CHROMOSOMES AT DIFFERENT EMBRYONIC STAGES IN *S. SIMILANS*

We may consider first the larval stages—comparing the diploid chromosome groups of the two sexes. A



Figs. 1-33. *Sciara similans*. Figs. 34 and 35. *S. pauciseta*? Figs. 36 and 37. *S. pauciseta*. Figs. 38-43. *S. prolifica*?



study has been made of the gonads of larvae at different stages beginning shortly after hatching and extending to the time of pupation. Figures in somatic tissues have not been favorable for study, so the observations are all on ovarian and testicular cells. Divisions may be found in the ovaries at all stages of development, owing to the proliferation of nurse cells and follicle cells as well as oogonia. In the testis the cells are at first practically all spermatogonia and later practically all spermatocytes. Spermatogonial divisions cease almost entirely at about the middle (?) of larval development when the spermatocyte growth period begins, the cells for the most part maturing almost simultaneously.

Our best male larval material has been obtained from larvae about one fourth to one third grown. In one lot of larvae (number 2,303)—all brothers from a pair mating from laboratory stock—a large number of spermatogonial figures were obtained. The lot includes both

All figures are from sections except 6, 7, 12-15, 17, 18, 22 and 25. The latter series and figures 34-43 are free-hand drawings. The magnification is variable in these outline drawings and is greater than in the others, which are drawn with the camera lucida, using 1.5 mm objective and number 12 ocular. Numbers in parenthesis are the slide numbers corresponding to those in tables 1 and 2.

Fig. 1. Ovarian chromosome group (2295).

Figs. 2-7. Spermatogonial chromosome groups (2303).

Figs. 8-15. Ovarian chromosome groups—8 (2295), 9 (2321), 10 (2299), 11 (2321), 12 (2314), 14, 15 (2296).

Figs. 16-18. Spermatogonial chromosome groups—16 (2325), 17, 18 (2299).

Fig. 19. Ovarian chromosome group (2316).

Figs. 20-24.\* Spermatogonial chromosome groups—20-22 (2316), 23, 24 (2318).

Figs. 25-27. Ovarian chromosome groups—25 (2311), 26, 27 (2328).

Figs. 28-33. Second spermatocyte groups—28, 29 (2362), 30-32 (2447), 33 (2364).

Fig. 34. Ovarian chromosome group (2465).

Figs. 35-37. Second spermatocyte groups—35 (2465), 36, 37 (2470).

Figs. 38-41. Ovarian groups—38 (2479), 39, 40 (2483), 41 (2489).

Figs. 42 and 43. Second spermatocyte groups—42 (2485), 43 (2489).

\* The drawing of Fig. 20 was lost in transti and the cut of the plate made before the absence of this figure was detected.

aceto-carminic smear preparations and sectioned material fixed in Flemming. From the latter alone 23 figures were sketched and several others examined. Four of these are represented in Figs. 2 to 5. Figs. 6 and 7 are free-hand sketches from two aceto-carminic smears. All the good figures in this lot exhibited the same chromosome group, *i.e.*, ten chromosomes—two short pairs, usually rod-like, two medium sized V-shaped pairs, and two unequal large chromosomes, one V- and one usually J-shaped. No good ovarian figures were obtained from this lot, but several were secured from other matings in the same stock. Nine of these are represented in Figs. 1 and 8 to 11 (from sections) and 12 to 15 (free-hand sketches from smears). They are taken from four separate matings in this stock and represent larvae at various stages of development.

We may now consider larvae—particularly male larvae—at earlier stages.

In the youngest larvae studied the gonads were about three cells in diameter and appeared to contain less than twenty cells. No figures were obtained from these. The next older were about five cells in diameter. These were so small that the sex could not be determined with certainty from the gross structure. In one of these five figures were obtained. Only one was favorable for counting the chromosomes. It is shown in Fig. 16 (from slide 2,325). In the other four figures the chromosome number was uncertain, but the two large chromosomes were evident.<sup>3</sup>

The difficulties of working with the above stages are almost prohibitive owing to the minuteness of the objects, and also to the fact that the sexes can not be distinguished except by the criterion of the chromosomes themselves.

At a slightly later stage the gonads begin to assume distinctive structural characteristics, although even here

<sup>3</sup> Female figures from the same bottle, at a later stage, show the usual four pairs of chromosomes and spermatocyte figures show the normal male group. See below under number 2,358.

they are only about eight cells in diameter (testes) and are practically invisible to the naked eye. Such gonads contain so few cells that usually many dissections have to be made in order to secure figures. Furthermore, in the testis at least, the cells seem to divide synchronously and it is only occasionally that they happen to be in metaphase. Consequently, it is a rare lot of material that includes good figures of both sexes, at the same stage, and from a single mother or a pair. (The difficulty is increased by the frequent occurrence of unisexual broods.) Two such lots have been obtained at this stage, however (numbers 2,299 and 2,316). In both of these the larvae are sibs from a virgin pair. In the first pair the parents are both from the same stock (the one considered above). In the second the father is from this stock and the mother is the daughter of a wild female taken in the same locality. In both cases the ovaries show four pairs of chromosomes and the testes ten chromosomes, as indicated by Figs. 10 and 17 to 22. Figs. 10 (♀) and 17 and 18 (♂) are from the first pair, and 19 (♀) and 20 to 22 (♂) are from the second. Figs. 17, 18 and 22 are free-hand sketches from aceto-carminic smears; the others are camera drawings from sections.

In another lot of larval material one aceto-carminic smear was obtained showing four figures (presumably spermatogonial) in one gonad. Each of these appeared to have only nine chromosomes. This was one of the first slides made of *Sciara* material and the writer was not then familiar with the chromosome groups, hence the possibility of error is large. It is not improbable that all ten chromosomes were present, and that one of the small ones was overlooked. In any event it is almost certain that both large chromosomes were present, for the notebook sketches all include them. The deficiency appears to be in the number of small chromosomes in each case. No other male figures were obtained from this lot, but three typical female figures were secured from another gonad. The latter was not identified as an ovary,

but subsequent observations make it safe to assume that it was.

In another lot of material (2,318) from young larvae three good spermatogonial figures were obtained from one testis. No female figures were found. This lot is from a virgin pair mating just like the one considered above under number 2,316. The female parents in the two cases are sisters and the male parents brothers. The good spermatogonial figures are all of the ordinary type, with ten chromosomes. Two are shown in Figs. 23 and 24 (sectioned material).

The above lots, from which spermatogonial figures were obtained, represent several stages in early larval development and consequently several generations of spermatogonia. During the latter part of the larval period no divisions (or practically none) occur in the testis. The spermatogonia have become spermatocytes. Maturation divisions do not begin until the time of pupation.

Since it is much easier to work with embryos at this later stage than in the early larval period and since at this time it is usually possible to distinguish male from female larvae or pupae before dissection, most of our chromosome counts of males have come from spermatocytes rather than spermatogonia. A series of spermatocyte metaphases is shown in Figs. 28 to 33. These and the large number of others studied (probably running into the hundreds all together) all agree in possessing six chromosomes, except in one case. In the latter one testis shows an extra chromosome (in at least some figures)—three large ones instead of two. Other testes from the same lot, however, have the normal six.

If all the chromosomes united in pairs the spermatocyte figures should contain five instead of six chromosomes. The presence of six is due to the fact that the two large ones appear separately on the spindle. Apparently these have not undergone synapsis as have the others.

In four of the spermatocyte figures (polar views) it will be noticed that one chromosome is drawn in outline only. This is because that chromosome lies at a different level, due to its precocious movement toward one pole, as shown in the two side views (Figs. 32 and 33). It is one of the medium sized V-shaped chromosomes, although the shape is not evident in all the drawings.

Numerous ovarian figures have been examined at stages corresponding to those in which spermatocyte divisions occur in the male. These are indistinguishable from the ovarian groups already figured and only two are shown here (Figs. 26 and 27).

#### COMPARISON OF CHROMOSOMES IN DIFFERENT WILD STOCKS OF *S. SIMILANS*

It has been shown in the preceding paragraphs that at all the embryonic stages studied in which the ovaries and testes can be distinguished from one another the cells in the testes possess two more chromosomes than those in the ovaries. It appears, then, that the sexual difference is constant throughout development, and we may next inquire as to its constancy in different wild stocks.

Some of the evidence on this point has already been given. The data as a whole may be summarized under two headings: First, the chromosome counts made from offspring of single females—either caught wild or taken from laboratory lines; and, second, the counts made from offspring in mass cultures. No differences have been observed between these two categories, but in the one case the flies are known to be sibs or half-sibs, while in the other their relationship is not so definitely known. Furthermore, this treatment permits a comparison of chromosomes in broods representing different sex-ratios (see earlier paper) and may serve for future reference.

#### CHROMOSOMES FROM OFFSPRING OF SINGLE FEMALES

In this category chromosome counts have been made from 30 different parentages, representing nine wild

sources. These all appear to belong to the same species, but it should be noted that not all have been definitely identified as such. A summary of the data is given in Table 1. An effort has been made to incorporate in this table all the pertinent data, including (1) the source of the parents, (2) their relationship if known, (3) the sex-ratio of the offspring which hatched (not including those dissected), (4) the kinds of chromosome groups examined, *i.e.*, ovarian, spermatogonial or spermatocyte, and (5) the mode of identification of the species, as well as the notebook record numbers of the matings and of the slides. In the identification column "s" indicates that specimens of that line were identified as *S. similans* by Professor Johannsen, or that they crossed with lines so identified. The letter "x" signifies that the two stocks cross, but have not been identified except by the writer. A dash indicates that no tests have been made.

Thirteen of the matings are from one line (stock 1) which comes from a wild-mass culture. All the other wild lines (last column) are from single wild females. Eight of the matings are from crosses of flies from number 49, or their descendants, with stock 1, and their origin may be explained briefly. Culture 49 represents a single wild female which gave 26 daughters and no sons. The chromosomes of one daughter are shown in Fig. 25. The records "49 × 62" and "49 × 46" represent outcrosses of single females from 49 with single males from stock 1. One such mating was number 75, and six of the records in the table come from this mating, or its descendants inbred or outcrossed. In the last seven matings in the table the male parentage is, of course, unknown, since each of these represents a female caught wild outside of the laboratory. All the collections of this species have been made on the laboratory grounds of the Carnegie Institution at Cold Spring Harbor, N. Y., in open sheds, pigeon house, etc.

Summarizing Table 1 it may be noted that female groups have been examined in offspring from 20 parent-



TABLE 1  
CHROMOSOME GROUPS FROM OFFSPRING OF SINGLE FEMALES (S. SIMILANS)

Culture.	Slides.	Figures examined.			Sex-ratio.*		Identi- fication.	Parentage.
		Ovarian.	Sper- mato- gonia.	Sper- mato- cyte.	♀	♂		
Stock	Smear	x		x	1	11	S	Stock 1.
84	"	x		x	0	11	S	"
85	"			x	0	11	S	"
94	"			x	8	25	S	"
96	"			x	25	8	S	49 × 54.
34	2299	x	x	x	0	2	S	Stock 1.
50	2312			x	4	19	S	"
29	2295	x			45	16	S	Stock 1. P <sub>1</sub> sibs.
30	2296	x		x	3	4	S	"
39	2303		x		26	0	S	"
49	2311	x			10	4	S	Wild ♀.
53	2313	x			2	4	S	St. 1. Virg. pr.
57	2314	x			33	0	S	" P <sub>1</sub> sibs.
92	2315, 6	x	x		31	19	S	Virg. pr. 49 × 62.
93	2320, 1	x		x	0	7	S	St. 1. P <sub>1</sub> sibs.
76	2318	x		x	20	0	S	Virg. pr. 49 × 62.
107	2328	x		x	16	1	S	" 49 × 46.
147	2362	x		x	43	3	S	Pr. from 75.
196	2438	x			11	0	S	Stock 1.
198	2436, 7	x		x	1	9	S	Pr. from 75.
197	2439	x		x	20	0	S	"
216	2443			x	11	0	S	Stock 1.
219	2447-9			x	1	9	S	"
239	2458	x		x	20	0	S	Vg. pr. 75 × 164.
260	2460, 3	x			99	1	S	203 × 212. Vg. pr.
247	2462	x			23	0	-	Wild ♀.
237	2464	x			22	0	-	"
245	2469	x		x	0	10+	-	"
285	2471	x					-	"
298	2476	x		x			-	"

\* Flies that hatched, not including those dissected.

ages, including 8 wild sources; that male groups have been examined in offspring from 18 parentages, including 4 wild sources, and that in eight cases chromosome groups from both sexes have been obtained from the same female parent. These include two separate wild sources and a cross between a male from one of these and a female from a third source. No attempt has been made to figure chromosomes from all these lines, since all conform to the types described above. The records in Table 1 are practically all from fixed and sectional material, except the first six.

#### CHROMOSOMES IN FLIES FROM MASS CULTURES

The data in this category are presented in Table 2. Here the flies are all from stock 1 or descendants from crosses between this stock and number 49, and are known to be *S. similans*. Summarizing the table it may be noted that ovarian figures have been obtained from six parentages and male figures from two parentages. In one case ovarian, spermatogonial and spermatocyte figures were obtained from the same lot. All these records represent sectioned material. Here again figures have been reproduced from only a few of the matings, since they are in agreement with the others.

TABLE II  
CHROMOSOME GROUPS OF FLIES FROM MASS CULTURES (*S. similans*)

Culture	Slides	Ovarian	Figures examined	
			Spermatogonia	Spermatocyte
97	2329	x	.....	.....
98	{ 2325 }	x	x	x
	{ 2358 }			
88	2364	.....	.....	x
188	2366	x	.....	.....
Stock	2368	x	.....	.....
214	2446	x	.....	.....
Stock	2450	x	.....	.....

## CHROMOSOMES OF SCIARA PAUCISETA FELT

The data on this species are less extensive and less satisfactory than those on either of the other two. We may consider first the preparations from offspring of wild female number 249, taken at Cold Spring Harbor, N. Y. Progeny of this female were identified by Professor Johannsen as being either *pauciseta* or a form very close to it. Presumably they are not *similans*, for specimens of that species were identified at the same time.

One good female chromosome group (Fig. 34) and eight less satisfactory ones were obtained from this lot. The good figure is indistinguishable from those of *S. similans*, except possibly for slight size differences among the chromosomes. The other figures all appear to have the same four pairs of chromosomes. A good series of spermatocyte figures was obtained from brothers of these females. They also are essentially like those of *similans*, *i. e.*, with six chromosomes, including the two large ones. One is shown in Fig. 35.

In preparations from the offspring of another wild female (262) which were definitely identified as *pauciseta*, no good female figures were obtained, but good spermatocyte groups were found. In one testis these contained seven chromosomes, *i. e.*, one more than in the other cases considered. The group consists of the two large chromosomes, the two medium sized V's and three shorter chromosomes, apparently all rod-like (Fig. 36). In another testis from the same lot (of brothers) some figures were of this same sort and others possessed in addition a third large chromosome, making eight in all (Fig. 37).<sup>4</sup> The slides have not been studied in detail, since our present purpose is merely to detect the presence or absence of the large chromosomes.

So far as the evidence goes, therefore, it supports the view that in *S. pauciseta* the sexes show essentially the same sort of chromosome difference as in *S. similans*.

<sup>4</sup> Evidences of degeneration are seen in some of these preparations and a high larval mortality occurred in some of the cultures, suggesting that the abnormal chromosome numbers may be due to morbid conditions.

CHROMOSOMES OF *SCIARA PROLIFICA* FELT

*S. prolifica* is a relatively large species not closely related to *S. similans* and *S. pauciseta*. Several wild females have been collected at Cold Spring Harbor, N. Y., all of which presumably belong to this species. The offspring of one were identified by Professor Johannsen, but no chromosome groups were obtained from this line. Descendants of another (number 255) were identified by the writer. It is not certain that the other lines belong to this species, but for present purposes this is not of prime importance, since the lines were kept separate and in three of them chromosomes groups from both sexes were obtained. These are numbers 242, 255 and 302. The chromosome counts are based on ovarian and spermatocyte figures, the dissections having been made too late to get spermatogonial figures.

Ovarian figures were examined as follows (all from sectioned material): In daughters of 242 five figures, all with four pairs of chromosomes. One is shown in Fig. 38. In daughters of 255 more than thirty figures suitable for counting, including nine suitable for sketching. All these figures likewise had four pairs of chromosomes. Two are shown in Figs. 39 and 40. In descendants of 302 the examination of ovaries was stopped after two good figures were obtained, one of which is shown in Fig. 41.

As may be noted from the figures the female chromosome group in *prolifika* is essentially like that of *similans*.

Spermatocyte figures were obtained in all three of these lines, but not in abundance. In line 242 only two or three figures were suitable for counting the chromosomes. These revealed the presence of six chromosomes, however, similar to those of *S. similans*, including the two large elements. In line 255 better figures were obtained, also essentially like those of *S. similans*. One is shown in Fig. 42. The same may be said for line 302. One chromosome group from this source is shown in Fig. 43.<sup>5</sup>

<sup>5</sup> Since the above was written, a large series of good spermatocyte figures in this species has been examined. They are almost identical with those of *S. similans*, except that the large chromosomes are both V-shaped.

In these spermatocyte figures the four smaller chromosomes resemble the four pairs in the female. The two large elements are similar to those in *similans*, but both may be V-shaped instead of one being J-shaped.

From these observations it seems safe to conclude that the chromosome groups of the two sexes in *S. prolifica* differ in essentially the same manner as in *S. similans*.

#### DISCUSSION AND SUMMARY

The descriptive data on *Sciara similans* have been given in considerable detail because most of the breeding experiments as well as most of the cytological observations have been made on this species. The observations on the other two species are merely confirmatory. Reviewing all the data together we may now consider the three features mentioned at the outset.

First as to whether or not the two "large chromosomes" in the male are true chromosomes: It has been shown that they are present in the spermatogonia from an early larval stage up to and through the maturation divisions of the spermatocytes. Consequently, it seems safe to conclude that they are constant and regular constituents of all the cells in the male throughout development. They have the characteristic appearance and behavior of chromosomes during mitosis. Their behavior during the resting stage and during the growth period has not been studied in detail, but they undergo certain changes in form, etc., comparable to those of the other chromosomes; *e.g.*, they have been observed in an attenuated, threadlike condition in prophases, contrasting later like the other chromosomes. Apparently they remain condensed through part of the growth period when the others are diffuse.

The evidence from spermatogenesis (not considered here) shows that they divide during the maturation divisions and go into some, if not all, of the spermatids. That they differ in some respects from the other chromo-

somes is clear, but the evidence all indicates that they are true chromosomes—as much so, for instance, as the ordinary Y-chromosome of most insects. Certainly they are not simply chromatoid bodies such as have been found in the spermatocytes of certain insects (Wilson, '13, *Biol. Bull.*, 24:392). Whether or not they bear any relation to the ordinary sex-chromosomes will be discussed in a later paper.

The second feature for consideration concerns the constant presence of these chromosomes in males and their absence in females. It has been shown that in all the material studied in which the sex could be determined—and this includes nearly all the material—the females lacked, and the males possessed, the two chromosomes under consideration. Since the observations on *S. similans* alone include something like sixty female individuals, from thirty parentages, and approximately fifty male individuals, from twenty-one parentages, it seems safe to conclude that the sexual difference is constant in these lines.

The third feature concerns the question as to how widespread this chromosome difference is. In *S. similans* the chromosomes have been examined in descendants from nine different wild females. All these have come from the same locality and in only a few cases have the chromosomes of both sexes been obtained from the same line (see Tables 1 and 2), but the consistency of the results in this series leaves little doubt that the difference is characteristic of the species. And the evidence is made all the more conclusive by the finding of a similar chromosome difference in the two other species, one of which is a close relative and the other a more distant relative of *S. similans*.



THE STRUCTURAL CONSEQUENCES OF MODIFICATIONS OF THE DEVELOPMENTAL RATE  
IN FISHES, CONSIDERED IN REFERENCE TO CERTAIN PROBLEMS OF EVOLUTION

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I. THE CONSEQUENCES OF MODIFICATIONS OF THE DEVELOPMENTAL RATE ON GROWTH AND ON DIFFERENTIATION

WHILE engaged in a series of studies<sup>1</sup> undertaken to determine the relation of environment to variation in fishes, the writer has been led to interpret certain physiological phenomena as significantly and factorily involved in structural evolution.

The central interpretation, the validity of which seems substantiated by the evidence embodied in this paper, is that those conditions, whether "external" (direct; individual) or "internal" (genetic; racial), which alter the rate of development,<sup>2</sup> affect the differentiation aspect of development in the same direction as the growth aspect. Conditions which accelerate the development rate accelerate and accentuate the differentiating tendencies, as well as the growth tendencies. Retarding conditions, on the other hand, retard and reduce both differentiation and growth.

As an example of this developmental phenomenon, the relation of changes in the rate of general development of fishes to the specific development of the scales may be cited. In the cases which have been studied, as the her-

<sup>1</sup> A number of these studies are not yet published. Those which have already been printed are referred to in the list of literature cited.

<sup>2</sup> The general influence of temperature on developmental rate is too well known to require special discussion here. Reference may be given, however, to papers on this subject by Johansen and Krogh (1914), and by Krogh alone (1914).

ring (Heineke, 1898; Ehrenbaum, 1909) and a number of cyprinids, percids and blennioids (Hubbs, Ms), it has been found that the formation (differentiation) of the scales is retarded or accelerated by those conditions which respectively delay or hasten growth. As a consequence, the scales do not appear until a larger size has been attained in slow-growing races or species than in the case of fast-growing forms.

The relation of growth and differentiation is evident in the main course of normal development. During the segmentation of the ovum there occurs a great multiplication of cells, but practically no growth; concomitantly, little differentiation. Subsequently the growth rate, as measured by proportionate increase, assumes its highest value. At the same time differentiation is enormously accelerated—more so relatively than the growth, for at given stages in early development the proportionate completeness of differentiation is greater than that of growth. Later in development the gradual decline in proportionate growth increase per unit time is accompanied by a decrease, relatively even greater, in the differentiation rate. These relations were discussed, from a different viewpoint, by Minot (1908).

In the present connection the well-known control by the thyroid incertion over both rate of metabolism and the rate of differentiation<sup>3</sup> (especially metamorphosis) should be considered. The effects of low temperatures in greatly retarding metamorphosis (*i. e.*, condensed differentiation) without having any apparent effect on the thyroid gland (Uhlenhuth, 1923, p. 318, and subsequent papers) seemingly fall into line with a very general tendency and do not appear to require the postulation of a "releasing mechanism" or "excretor substance."

In agreement with this central interpretation that conditions modifying the development rate affect differentiation in the same direction as growth, it apparently usually holds true that accelerating conditions more

<sup>3</sup> For a very recent discussion of this problem, see Budington (1925).

quickly, more abruptly and to a greater degree affect the general slackening of the growth rate with age than do conditions retarding the development rate. Thus Lehenbauer (1914) found that the rapid initial rate of growth of plant seedlings under high temperatures is not long maintained, whereas the slow initial growth under low temperatures is maintained even under prolonged exposure. Similar relations often if not in general hold for the whole life-cycle of fishes. Pütter (1920) recently made a strained effort to explain this situation in terms of the "simplest possible physico-chemical phenomena." His treatment of the subject was largely deductive, and in deriving his formulas for the computation of growth at different temperatures he made a number of assumptions which seem unwarranted. As a culmination of his deductive mathematical analysis, he arrived at the surprising conclusion that a positive growth increases up to a certain point (the greatest size being attained at  $0^{\circ}\text{C.}$ ), beyond which a negative growth period obtains, causing the animal to return, death not intervening, toward a zero size.

Pütter's deductive analyses do not seem to invalidate the following interpretation of the reason why retardation of growth with age occurs more quickly and is more abrupt and extensive under accelerating than under retarding conditions of development. Under any conditions which accelerate development, the early growth is fully accelerated, by reason of the fact that inhibitory tendencies have not yet been brought into effective action. The later growth, on the contrary, is relatively very extensively retarded, because the development of inhibitory tendencies, like other controls of differentiation, is also hastened and accentuated. The general growth inhibitions, as is well known, often are associated with the ripening of gonads, the attainment of maturity being marked by a cessation of growth in warm-blooded animals, and usually by a sharp decline in the growth rate in the case of fishes and other animals exhibiting indeterminate growth. Accelerating conditions hasten the

inception of maturity and the associated decline in growth rate.

The abrupt and extensive retardation of growth under accelerating conditions of development explains the general observation that fishes of cold or saline waters usually attain a larger size than do individuals or races of the same species inhabiting warm or brackish water, or both (see Möbius und Heineke, 1883). This principle usually holds true despite the great shortening of the growing season in northern waters<sup>4</sup>, a condition which is probably responsible for nearly all the apparent exceptions to the general rule. The exceptions are spoken of as apparent, because they would not appear as such if the growth were expressed on a *per diem* rather than on the physiologically less significant seasonal basis. As a very general rule the warm-blooded vertebrates also increase in size toward the north (Allen, 1871 to 1877).

This reversed action of differential acceleration on early and on late development apparently applies not only to the entire development, but also to any stage thereof which involves growth and is brought to a close by inhibition. Thus it is very generally true that, in those individuals or races of fishes which show an accelerated embryonic development, the addition of somites—which is practically synonymous with the growth of the embryo—proceeds much faster than in those individuals or races of the same species subject to or exhibiting a relatively retarded development, but the increase, like that of growth in general, terminates relatively sooner and more abruptly. As a final consequence, warm or brackish water representatives have as a very general rule fewer vertebrae than do individuals or races of the same species inhabiting water of lower temperature or higher salinity.<sup>5</sup>

<sup>4</sup> In northern Michigan, for example, Dr. C. W. Creaser and the writer found that the growing season of fishes scarcely extends beyond the four months of June, July, August and September.

<sup>5</sup> This phenomenon is the special subject of a series of papers published (Hubbs, 1922, 1924a, 1925) or being prepared by the writer. Space will not permit the discussion here of the data and literature bearing on this problem.

Modifications in segment number of fishes may also be associated with differences in development rate, which, unlike those just discussed, are not interpretable as metabolic adaptations to the environment. For example, the retardation of development brought about by the deposition of an unusually large amount of yolk in the ovum often is correlated with a great increase in segment number. Thus most elasmobranchs and chimaeras as well as many genera of teleosts, as, for instance, *Synbranchus*, have very large eggs and very numerous segments; a review of the data will be presented in a future paper. A protracted development associated with viviparity, in the Embiotocidae or viviparous perches of California (Eigenmann, 1894a; Hubbs, 1921c), is correlated likewise with an increase of vertebral number. Similarly, the slowing down of development, conditioned by the insertion into the life-cycle of that peculiar larval-postlarval adaptation to pelagic life which finds its extreme expression in the leptocephalus stage of the eels, seems to bring about an increase in the number of segments. Such larvae or postlarvae—inordinately elongated and compressed creatures having the muscle replaced by gelatinous tissue—contrast sharply with the compact, muscular and often spined or armored early stages of fishes having an accelerated larval development accompanied by a low number of segments. An examination of the extensive literature dealing with the early development of fishes indicates that probably all the numerous spiny-rayed fishes possessing the characteristically low and basic vertebral formula,  $10+14=24$ ,<sup>6</sup> almost certainly all with the total number reduced below 24, and many with the number but slightly increased beyond 24, pass through a markedly abbreviated development.<sup>7</sup> These cases of cor-

<sup>6</sup> An excellent discussion of the evolutionary significance of this basic vertebral formula of the acanthopterygian fishes is given by Boulenger (1905).

<sup>7</sup> The limits of the present paper do not permit a detailed discussion of the extensive literature and data bearing on the early development of fishes. It is planned to deal with the problem in another paper.

relation between rate of development and the number of segments are far too numerous and clear-cut to be passed by as coincidences.

The relation between differential rate of development—whatever its basis may be—and the number of vertebrae eventually produced becomes particularly apparent in the comparison of related forms. Thus the spring-spawning races of the European herring have fewer segments than the autumn-breeding types, and a more accelerated development (Heincke, 1898; Ehrenbaum, 1909). Similarly, the race of anchovy inhabiting the brackish waters of San Francisco Bay has fewer vertebrae and a less protracted development than the typical *Engraulis mordax* of the adjacent ocean coast of California (Hubbs, 1925). The European eel develops more slowly than the American species, and has more segments (Schmidt, 1922). *Argentina silus* has more segments than *Argentina sphyraena*, and a more protracted early development (Schmidt, 1906). *Agonus cataphractus*, with 36 vertebrae, has a much less extended development than *Leptagonus decagonus*, which has 45 vertebrae (Schmidt, 1908). Many other cases show a like correlation between rate of development and number of segments.

Those fishes which pass through a protracted development usually show an extenuation not only of growth, but also of those age differentiations in form which result from the differential rate of growth in various parts of the body. They usually have, for instance, proportionately shorter heads and smaller eyes than related forms (or individuals) of more accelerated development, the normal age changes in the proportions of these parts being carried to a farther degree. These changes take place, whatever be the underlying cause of the retardation in development, whether the coldness or salinity of the water, or an increase in the amount of yolk material in the egg, or a gelatinous specialization of the early stages. The changes seem to occur when the basis of retardation is individual, as well as when it is genetic.



Fishes of retarded development frequently show, also, an increased development of those modifications of the skin, such as cirri, bony plates and spines, which appear at a relatively late stage.

This increase in differentiation of form and of dermal structures in the later part of development, under retardation conditions, is not merely proportionate to the extenuation of growth rate; it is evident sooner in reference to general development. Thus not only at the larger sizes attained, but also at comparable sizes, the head and the eye are proportionately reduced. This general phenomenon lines up with the central interpretation that differentiation is affected in the same direction as growth by conditions altering the development rate. In this case the action of differentiation controls (inhibitions) is obviously hastened and accentuated in accelerated development.

The decrease in the late differentiation of fishes of accelerated development was appreciated as early as 1883 by Möbius and Heineke, who wrote (1883, p. 184):

Bei marinen Arten wirkt die Anpassung an das Brackwasser in einer ganz bestimmten Weise verändernd und zwar bei allen Arten in gleicher Weise. Schon bei der Charakteristik der nordöstlichen Ostsee sind Andeutungen hierüber gemacht.

1. Die Brackwasserrassen sind kleiner, ihr Rumpf ist höher, die Bewaffnung des Körpers mit Stacheln und ähnlichen Hautbildungen ist schwächer. Letzteres zieht sich namentlich bei dem kleinen ungepanzten, kurzstacheligen *Gasterosteus leiurus* im Gegensatz zu dem grossen, gepanzerten, langstacheligen *trachurus* ferner bei den in Brackwasser lebenden Individuen von *Cottus scorpius*. Noch besser werden wir diese Thatsachen ausdrücken, wenn wir sagen: Die Brackwasserrassen werden auf einen jugendlicheren Stadium geschlechtsreif, als die Salzwasservarietäten derselben Art. Nach den Erfahrungen am Heringe zu urtheilen, ist eine Hauptursache dieser Verschiedenheit die schnellere Entwicklung der Eier und der ausgeschlüpften Brut im Brackwasser, welche wiederum durch physikalische Verhältnisse, wie geringe Tiefe, höhere Temperatur, intensiveres Licht, geringeren Salzgehalt an den Laichplätzen und schwachere Bewegung des Wassers bedingt sein wird.

The data used as the basis of these principles were in part elsewhere published by Heineke, in his classical study on the races of the herring (1898), in a paper on

the Gobiidae and Syngnathidae (1880), and one on *Gasterosteus* (1889). Rutter (1896), Regan (1909), Snyder (1908) as well as Heincke, have remarked on the weak development of armature and spines in the freshwater forms of *Gasterosteus*, and have observed that changes which take place from the north to the south on the one hand, and from the sea into fresh-water on the other hand, are similar. Roth (1920) also noted a southward decrease in the number of plates in *Gasterosteus* and found that the plates progressively lost are the last ones ontogenetically developed, those first formed being racially most permanent.

In the most extensive racial investigation of fishes ever undertaken, Johannes Schmidt (1917a, 1917b, 1918, 1920, 1921; see also Smith, 1921) has found that a decrease in form differentiation and particularly in segment number of *Zoarces viviparus* generally takes place from the ocean into warmer and brackish fjords, and that the differences, although genetic, may also be experimentally altered to a slight degree<sup>s</sup>.

The writer has found that most of the cottoid fishes of the open California coast show a gradual decrease toward the south in size and in form differentiation as well as in segment number. This case is of interest in showing that these modifications may be determined by changes of temperature as well as of salinity (see Huntsman, 1919), or by the combined action of both factors.

In the Atherinidae modifications similar to those observed in general have been found, a reduction in segment

<sup>s</sup> The individual differences induced by Schmidt were of the opposite environmental correlation as compared with the racial differences. Individuals brought from the ocean outside into a fjord, and kept confined in live-boxes, produced offspring having a number of segments slightly (but significantly) lower, not higher, than either their parents or the mean race to which they belonged. In other words, water conditions which ordinarily induce accelerated development were here associated with such results as are usually produced by retarded development. But in this case the imprisonment of the viviparous fishes in the live-boxes may have reduced the metabolic activity of the mother and hence the developmental rate of the young. In this way an increased number of segments might have been induced.

number or in differentiation of form taking place toward fresh-water (Roule, 1902, 1903a, 1903b), toward the south in the Northern Hemisphere (Kendall, 1902; Hubbs, 1918; Jordan and Hubbs, 1919, p. 57-58), and toward the north in the Southern Hemisphere (Jordan and Hubbs, 1919, p. 15, 17, 66). In an Australian fish, *Retropinna*, in which McCulloch has found that similar differences occur, the variation is similarly in the opposite actual direction to that observed in the Northern Hemisphere, but in the same direction in temperature gradient. Many other instances of a confirmatory nature might be cited. A more extended discussion of the ichthyological data bearing on these problems will be presented in other papers.

#### APPARENTLY CONTRADICTORY CASES

Certain apparent exceptions to these general variational trends have been stressed by certain authors. Most such cases are those in which the environmental correlation seems to be the opposite of that admittedly usually shown. These require discussion at this time.

Schmidt has presented evidence to show that the inherent properties of the organism play a rôle of greater importance than the environment in such minor evolutionary processes as are here being discussed. Two of the instances cited by this author involve the number of segments of the clupeoid fishes. While it is generally obvious that the number of segments in *Clupea harengus* decreases toward warmer and less saline waters, Schmidt points out that the White Sea herring is characterized by an incompatibly low number. But this race seems to belong to another species, the Pacific herring (*Clupea pallasii*), as indicated by us, and it has more vertebrae than the British Columbia race of that species, which in turn has more segments than the California form (Hubbs, 1925). Again, Schmidt points out that the related sprat (*Sprattella sprattus*) in the Baltic region seems to vary in a direction opposite to that there exhibited by *Clupea*

*harengus*. But later work has not confirmed this evidence: probably annual variations exceed the geographic in the sprat (see data in Fage, 1920).

Schmidt furthermore lays much stress on the fact that the variations in *Zoarces* are not perfectly correlated with environmental factors, and dismisses, we think without good reason, the possible differential action of varying combinations of temperature and salinity. As a whole, however, Schmidt's elaborate data on *Zoarces* show conclusively that the segments decrease in number toward relatively warm and brackish water. As the evolution process seemingly involves the parallel selection of mutations, the surprise is that the relation of the characters of the races of *Zoarces* to their respective environments is as definite and close as Schmidt has shown it to be.

Cox (1923) has lately shown that a stickleback, *Apeltes quadracus*, shows an increase in the number of dorsal spines in the portions of the Gulf of St. Lawrence characterized by reduced salinity and increased temperature. This variation appears to have the opposite environmental correlation to that shown by other fishes in the same area. Cox (1903) earlier indicated that four species of flounders all showed in these shore waters a decreased number of fin rays and vertebrae as compared with their truly marine representatives, and Lea's data (1919) indicate that a similar trend of variation is shown by the herring in the same waters.

Certain fresh-water fishes show a decreased rather than an increased number of rays, in one of the vertical fins, in water of reduced temperature. Thus Schmidt (1919a, 1919b) has shown that the number of dorsal rays of the viviparous poeciliid *Lebistes reticulatus* is reduced in fishes developed in cold water. Despite this individual modification, small differences in ray number were found to be inherited. In the case of two related fishes, both of Middle America, *Pseudoxiphophorus bimaculatus* and *Priapichthys annectens*, we have recently shown (1924b)

that the number of dorsal rays decreases from the *Tierra Caliente* to the much cooler mountain streams. In an American minnow, *Notemigonus crysoleucas*, a somewhat similar variation is shown; in this case, however, involving the anal fin: the number of anal rays gradually decreases, in the average, from 15 to 11, in passing from Florida to Minnesota (Hubbs, 1921a). More extensive data, now at hand, emphasize the gradual nature of this variation, a decrease of one ray taking place each four hundred miles. The lines formed by joining localities with an equal ray number agree remarkably well with the spring isotherms, even including the southward dip in the Appalachian Mountains. A somewhat similar though much less regular correlation between temperature and anal ray number perhaps lies at the basis of the remarkably wide geographical variation exhibited by the Northwestern American minnow *Richardsonius* (for data see Eigenmann, 1894b, 1895; Gilbert and Evermann, 1894). In all these cases the exceptional variational trend seems to involve only the one fin, not the number of vertebrae, or other characters. No explanation of such cases can be offered now.

Another alleged instance of reversed environment correlation in such variations is that of the crustacean genus *Chiridothea*. Ekman (1919) has claimed that this "relict" form shows a character-gradient from salt water to fresh water exactly the opposite of that exhibited by other relict crustaceans. *Mysis oculata*, *Gammaracanthus loricatus* and to a lesser degree *Pontoporeia affinis* suffer a decrease in form differentiation in the salt-water to fresh-water series. The *Chiridothea*, on the other hand, is held to exhibit, in the same series, an increase in form differentiation, the adult being more extreme than the adult of the marine type, rather than, as in the other cases, resembling the young of the marine form. It must be noted, however, that there is reason to believe that the marine species cited (*sibirica*) is not, as Ewman claims, the "Stammform" of the brackish and fresh-water species

(*entomon*). The great differences in the size of the lateral expansions of the thoracic segments and in the shape and armature of the telson, exhibited in the young from the brood pouch, suggest that these species are not very intimately related: in these respects the young diverge more than the adults. Such being the case, the propriety of uniting these species into a single form-series may legitimately be challenged.

It is evident that some of the cases discussed above are not valid exceptions to the general principle under discussion. On the other hand, it is quite as clear that exceptions do exist, and in many other instances the correlation of characters with environmental factors is either lacking or highly imperfect and irregular. Indeed such principles can not be expected to be of invariable application. It seems quite safe to conclude, however, that the later differentiations in form and structure are in general carried farther under retardation conditions of development than under acceleration conditions.

## II. THE BEARING OF THESE PHENOMENA ON SOME PROBLEMS OF EVOLUTION

### (a) *The Problem of Adaptation*

As already indicated, modifications in the rate of development may entail definite structural changes. These modifications, when exhibiting a definitive environmental correlation, seem best interpretable as physiological adaptations. The adaptations may or may not be genetic: when direct, individual and external, the adaptation would be explainable in direct physiological terms; when indirect, racial and internal, the adaptation might well be regarded as the genetic modification of a developmental factor—the selection, perhaps, of a metabolic mutation. The adaptation would involve the genetic retardation of the developmental rate in those races habitually subjected to such environmental factors as individually retard development; or, the genetic acceleration of the developmental rate in those races ordinarily surrounded



by media which induce accelerated development in the individual. Thus subjection to waters of low temperature and high salinity either directly and individually, or indirectly and genetically, induce a retardation of development in fishes. The effect of either higher temperatures or decreased salinity is in the opposite direction. In either case the development modification is correlated with definite structural changes.

In other instances the modification of early physiological activity and developmental rate and the corresponding structural consequences have a basis in genetic changes in the amount of yolk in the egg or in the character of the tissues of the larval stage. In these cases the relation of the adaptation to changing environmental factors is at once obscure and indirect. Such adaptations meet primarily developmental rather than environmental needs.

The structural consequences of alterations in developmental rate involve the number of vertebrae, scales and fin-rays, the proportions, the development of dermal outgrowths, etc. These changes are often slight, only to be determined by statistical means, or they may be large. Most structural modifications of this type have usually been interpreted as being without adaptive significance, and partly on this basis, systematists in general hold that characters most serviceable in classification are of the non-adaptive type (see for instance Jordan, 1906). But many such modifications seem to be the direct consequences of physiological adaptations. Morgan (1923, 1924) has lately suggested, from a standpoint of genetics, that many apparently non-adaptive structural features may be produced by adaptive physiological modifications.<sup>9</sup> The rôle of adaptation in evolution is probably more extensive than it has generally been held to be, in recent years.

<sup>9</sup> Julian Huxley advanced this point of view, obviously in terms similar to those adopted in the present paper, in 1922 (see *Nature*, Vol. 110, No. 2770, December 2, 1922).

*(b) The Problem of Speciation*

The structural consequences of differential rate of development, as indicated in the foregoing discussions, probably comprise a considerable proportion of the characters differentiating local races among fishes, and perhaps many of the distinctive features of races in other groups of animals.

*(c) The Problem of Degeneration*

The interpretation of certain types of structural evolution as the definitive consequences of physiological mutations, if valid, render more definite our conceptions of the processes involved in evolutionary degeneration.

Evolutionary degeneration resulting from accelerated development is not usually if ever very extensive, although frequently evident, and perhaps quickly and readily brought about. Degeneration with this basis seems to involve chiefly the elimination of the final stages in differentiation of form and of dermal outgrowths, such as cirri, bony plates and spines. This elimination, as already stated, is the apparent consequence of the advancement and accentuation of the effective inhibitions. Degenerate forms so produced, if indeed they may legitimately be so named, are merely juvenile in their characters. Instances of such degeneration have already been given.

Degeneration correlated with decreased physiological activity and retarded development is in contrast apparently less readily and quickly consummated, but may be much more extensive, involving the elimination of final stages of early differentiations, these as a whole being more fundamental and extensive and more numerous than the late differentiations. This elimination is apparently the result of the parallel effects of retardation on differentiation and on growth. The appearance of the differentiations may be so greatly delayed as to be carried beyond the limit of the normal life-cycle. More frequently, however, their appearance is only delayed until

a time when conditions of general size, thickness of skin or ossification of bone, etc., preclude further differentiation.

Conspicuous examples of such degeneration correlated with retarded development, involving the retention of embryonic (as opposed to juvenile) characters, are to be found among the fishes. Mention may be particularly made of the retention of an open lateral line tube in fishes of exceedingly slow development, as the Chimaeridae and certain deep-sea teleosts, of a partially heterocercal caudal fin in the salmonid and coregonid fishes, of a semi-cartilaginous skull in the same and other groups. In all these cases the process of differentiation remains uncompleted in the adult. Similarly, when the squamation remains incomplete in the adult of forms with retarded development, those scales which are first lost in degeneration are those last formed in normal ontogeny. In those cases in which differences in completion of squamation appear within the species, the relation between the elimination of the final stage in scale formation and the retardation in development is particularly evident. It has been found, for instance, that in the more slowly developing races of several darters and a minnow, that the scales occasionally fail to cover the nuchal region, which is the last to be scaled over in ontogeny. In a Pacific coast blenny of retarded development, *Anoplarchus purpureus*, in which scales never develop at all on the trunk, the forward extension of the scales is greater to the southward than to the northward<sup>10</sup>.

Degeneration resulting from altered developmental rate, it thus appears, involves the elimination of final stages in development, this being done in such a way that accelerated development involves the retention of juvenile features, while retardation involves the retention of embryonic characters. Degeneration of this type, as here interpreted, does not primarily nor necessarily involve

<sup>10</sup> A fuller account of both these instances will appear later in other papers.

any direct genetic loss, but involves physiological adaptations which preclude the completion of certain ontogenetic processes.

(d) *The Problem of Progressive Evolution*

It is indicated in the foregoing section that the rôle of physiological adaptation is apparently not limited to the racial elaboration of the ends of evolutionary lines, apparently entering also into the process of extensive degeneration. It remains to be considered whether these physiological adaptations may be interpreted as significantly involved in progressive evolution.

An accelerated development, as pointed out in earlier parts of the paper, results in emphasis of the early differentiations, which are the most important in determination of the most essential characters of the adult. Obviously, however, the increase of differentiations must soon reach a genetic limitation, for all definitive differentiations must have a genetic basis. But acceleration may furnish a condition receptive to the introduction of new differentiations originating by mutation—thus contrasting with retardation, which might mitigate against the introduction of new differentiations. In agreement with these interpretations we find that those fishes which have a rapid development, as contrasted with those having a slow development, in general show a relatively higher degree of differentiation and specialization.

Physiological adaptations, which are probably the chief bases of differential rate of development, appear therefore to be significantly, although probably indirectly, involved in progressive evolution.

The evolutionary consequences of physiological adaptation on these assumptions would be analogous to those of natural selection. They apparently do not primarily or directly involve the origin of variations, but provide a means for their fixation and perpetuation. We should not overlook the possibility, however, that a high rate of metabolic activity may in some way lead to increased production of new heritable variations (mutations).

(e) *The Problems of Phylogeny*

Extensive degeneration, involving the retention of embryonic features, has here been interpreted as often a consequence of greatly retarded development. If this interpretation is valid, it follows that this phenomenon presents a means of testing whether simplicity of structure in a given group is a primitive or a secondary feature. The test would involve determining whether the development is or is not greatly retarded. For instance, the excessively slow development of the salmonoid fishes adds weight to the interpretation of the semicartilaginous skeleton, the partially heterocercal tail, etc., as secondary features, and to the consequent allocation of the group well within the teleost series, rather than between the ganoids and the teleosts. In this case, paleontological evidence is strongly confirmatory of the interpretation of relationships here made.

If the interpretations advanced in the previous sections of this work are valid, it would further follow that we have in the cases discussed a key to the determination of the direction and possible reversibility of the evolutionary processes involved. It appears probable that evolution of structure and form as conditioned by the modification of developmental rate through physiological adaptation or otherwise, may proceed in either a given direction or in the opposite direction (for example, either toward or away from a juvenile condition). Thus the southern derivatives of northern types of fishes are usually modified in the same general features as are the northern representatives of warm water types, but in the opposite direction.

It seems true also that structural evolution controlled by alterations in developmental metabolism is reversible. This possibility has not been considered by certain authors, as Smitt (1886, 1895, 1901a, 1901b) and Fage (1911), who have attempted to postulate the direction of speciation, nor by Jordan (1891, 1893) or Boulenger (1905) in their discussion of evolutionary changes of seg-

ment number. Thus we find that northern types of fishes which already have assumed such characters as are usually associated with and probably determined by a retarded development, become racially modified in the opposite direction after having reentered bodies of water which condition an accelerated development. The change is toward the original characters of the warm water ancestors of the northern types. The case of *Zoarces*, so elaborately investigated by Schmidt (1917-1921) is particularly clear. The typical basic race of the North Atlantic waters is characterized by features of form and proportions and the high number of segments associated with cold-water conditions. The numerous fjord races obviously evolved from this ocean race, and, living in water of increased temperature and decreased salinity, show modifications in form and proportions which slightly approach the characters of the more typical spiny rayed fishes of warm waters, from some one of which the zoarcid fishes must have sprung. The fjord races also show consistently a decrease in the number of vertebrae, which again marks a reversion toward the original warm-water ancestor of *Zoarces*.

This reversibility of such structural evolution as is determined by physiological adaptation would indeed be expected, if the interpretations of the present paper are valid. If alterations of developmental rate, as here assumed, determine certain definite structural changes, then a reverse metabolic adaptation would induce reverse structural changes. It might be expected that the reversibility would be very close and exact for the smaller evolutionary changes, as the loss of characters due to changed rate of development seemingly involves inhibitory actions of some kind, rather than, necessarily, genetic losses. A reverse metabolic mutation might automatically eliminate the inhibition, and permit the remanifestation of characters temporarily concealed along the phyletic line.

The strong probability of evolution leading either toward or away from the development of juvenile charac-



teristics in the adult, and of the process being reversible, makes it appear quite improbable that the biogenetic law applies in these cases. Of two related races or species, the one possessing characters diverging the less from the juvenile condition is not necessarily more primitive than the other or ancestral to it, as Smitt has consistently held in his fish studies (1886, 1895, 1901a, 1901b). The more juvenile of the two types, as for instance any of the fjord races of *Zoarces viviparus* (investigated by Schmidt), or of the similar fjord or estuarine representatives of many other ocean species of fishes, is in reality probably more frequently derived from, than ancestral to, the marine type which diverges to a greater degree from the juvenile condition. The biogenetic principle perhaps can not be applied at all to such evolutionary processes as are discussed in the present work.

### III. SUMMARY

The central interpretation advanced in this paper is that either individual or racial modifications of the developmental rate affect the differentiation aspect of development in the same direction as the growth aspect. Conditions which accelerate the developmental rate accelerate and accentuate the differentiating tendencies as well as the growth tendencies. Retarding conditions operate in the opposite manner. This relation of growth and differentiation is evident in the course of normal development.

Accelerating conditions hasten growth in the early stages, but later bring about a slackening of the growth rate, probably because of their accentuated action on growth inhibitions. Retarding conditions cause a protraction of the early growth, but a less abrupt slackening of the growth rate with age, so that eventually the size attained is often greater than under accelerating conditions.

Similarly, the addition of somites, which is practically synonymous with the growth of the embryo, proceeds

faster under accelerating than under retarding conditions of development, but terminates relatively sooner and more abruptly. As a consequence, warm or brackish water forms of a species of fish have as a general rule fewer vertebrae than the forms inhabiting cooler or more saline water. An increase in the number of segments is also associated with protracted development having a basis in a great increase in the amount of yolk in the egg or in the larval-postlarval modification to pelagic life in which the muscle is replaced by gelatinous tissue.

Fishes passing through a protracted development often show an extenuation of age differentiation in form as well as of growth. Their proportions depart more from the juvenile conditions than do those of fishes going through a more hurried development. They often show also an increase in dermal modifications, as cirri, plates and spines. This increase in differentiation is more than proportionate to the extenuation of growth; at comparable sizes, the fishes passing through the contrasting types of development show these differences. The action of differentiation controls (inhibitions) is obviously hastened and accentuated under acceleration conditions.

Some supposedly contradictory cases are shown to be based on erroneous observations. Others, however, are valid, but can not be explained at present.

*The problem of adaptation.*—The modifications of developmental rate entailing definitive structural consequences seem best interpretable as physiological adaptations. When genetic, the changes in developing rate may be regarded as due to the selection of metabolic mutations, or to egg or larval modifications. Many of these structural consequences of physiological adaptations are among those characters of high systematic value long thought to be specifically devoid of adaptational significance. The rôle of adaptation in evolution is probably more extensive than has generally been postulated.

*The problem of speciation.*—The structural consequences of differential rate of development probably com-

prise a considerable proportion of the characters differentiating local races of fishes.

*The problem of degeneration.*—Degeneration resulting from accelerated development consists merely in the retention of juvenile characters. Degeneration correlated with decreased physiological activity and retarded development may be much more extensive, involving the elimination of final stages of *early* development and the retention of embryonic as contrasted with juvenile characters.

*The problem of progressive evolution.*—Accelerated development results in the emphasis of early differentiations, and seems to provide a means for the fixation and perpetuation of variations leading toward specialization.

*The problems of phylogeny.*—The interpretation of degeneration being associated with protracted development offers a means of testing whether simplicity of structure is a primitive or secondary feature. The general interpretations of the paper indicate that structural evolution controlled by alterations in developmental metabolism is approximately or even exactly reversible. Such changes involve particularly modifications of the adult toward or away from juvenile characteristics. If such changes are reversible, as seems highly probable, then the biogenetic law does not apply.

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## FACTORS OF FISH CLASSIFICATION<sup>1</sup>

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SINCE the beginning of fish classification there has been a constant rearranging of groups. Not only have they been shifted about from one relationship to another, but there has been an incessant dividing and merging of them and a changing of group values.

The great wealth of forms that comprises the class fishes is, of course, only the end products or tips of the diverging branches that represent the lines of descent. But between them there is interlaced a network of puzzling characters that has made their classification very unsatisfactory. Some of the branches naturally reach much farther back towards the main trunk than do others, for in the comparatively unvarying conditions of aquatic life we find especially well marked the condition of life, on the one hand, apparently undergoing rapid changes, and, on the other, life almost unchanging. Certain primitive forms still exist that seem to have had their characters fixed in very early geologic ages and to have remained with little change since that time. With them, apparently under similar conditions, are recent forms, some of which, to judge by the multiplicity of close relations with variable and intermediate characters, seem to be in an unsettled formative state.

The relationships between the fishes has been less satisfactorily worked out than it has been between the members of any other class of vertebrates. This is not because they have been neglected, for they have received as much attention as any other class—perhaps more—by a surprising number of master minds of the past.

<sup>1</sup> Read at the Los Angeles meeting of the Pacific Division of the American Association for the Advancement of Science before the Western Society of Naturalists, September, 1923.

Life on the land leads to more diverse form of body than life in the water, with the result that aquatic-living vertebrates have approached more nearly a common form. Hence the fact that fishes have the same general form may cause us to feel close relationship between them when little may actually exist. This influence of aquatic life toward uniformity of body form is well shown in those land-living classes that have secondarily taken to aquatic life and adopted a fish-like form. Thus, among mammals, the porpoises are as fish-like in form as the fishes themselves, even to the modification of the fore limbs back to fins, the development of analogous dorsal fins and a propelling caudal. Among extinct reptiles there were many examples showing the same fish-like forms with fish-like fins. Even among such diving birds as the penguins something of the same thing appears. They have all in some degree approached the lines that marine engineers use in designing ships—the “entering angle” being in definite correspondence to the “run.”

We treat the class fishes just as we treat the other classes, expecting them to respond in the same way and forgetting that the class is practically as old and the sum of development as great as all the other vertebrate classes together. While the fishes have remained fishes, externally changing very little as compared with other vertebrates, the amphibians, reptiles, birds and mammals have descended from them with all their diversified forms and with all the countless intermediate forms disappearing.

In the class Mammalia we find that similarity almost invariably means relationship. Even habit, as carnivorous or herbivorous, coupled with the anatomical modifications that naturally accompany it, shows relationship. But here we are dealing with a comparatively recent group, one that is not old enough to have passed through all the multitudinous generations that the fishes have. Could we have taken the fishes when the group was no older than the group of the mammals probably we could

more truly have read and valued their characters, and could have arranged them with all the confidence of being correct that we feel in regard to the mammals.

The fishes have passed through just as many countless generations as the birds and mammals have, since they, too, were aquatic primitive chordates. The same vast interval of time has passed, and the same vast number of variable forms have been produced, whether or not they have remained little changed or have become highly specialized. The changes may not have been so great, but for that very reason they have been more puzzling to the anatomist and taxonomist. But we have the same attitude when we compare two fishes that we have in comparing two forms of any recent class of vertebrates, though our two fishes may be separated by countless generations produced through an enormous stretch of time.

Thus we may make the rule that the more recent the class the easier its classification, and the clearer its intra-relationships.

In the beginning the fishes were arranged according to external form and external characters. This served for a considerable time until the attempt was made to go deeper and prove relationship by anatomy, particularly osteology. Generally, the result was in the direction of improvement, especially if internal characters were coordinated with external ones. But often the investigator relied so much upon his discoveries in osteology that he ignored other characters; usually with chaotic results.

Lines of descent in fish groups are difficult to appreciate because of our inability properly to weigh and value one character against another. A fish may have a character which is shared by certain other fishes. This might guide us to its relationship with some exactness, were it not that it will probably also have another character that might equally well indicate a totally different relationship. It is not at all uncommon to find several conflicting characters, each calling for a different relationship, and each seemingly of considerable importance. The investi-

gator is then driven to choosing between characters and must rely largely upon his intuition, and upon his experience and knowledge of the value of these characters in other fish groups. To make the situation more difficult, a certain character in one group which seems to have great importance and stability appears in another group to lack stability and to be worthless in indicating relationship. Of course at times characters appear that are not puzzling, and because they coordinate so well with all conditions and probabilities we feel that they are certain indicators of relationships. It is such rewards that one is ever hoping to find.

The importance of distinguishing between general characters has been little appreciated. All characters held in common do not necessarily mean very much in the consideration of relationship. Often the investigator will publish a long comparison between two or more fishes to prove relationship between them, listing at great length all the points of similarity without appreciating that he is merely listing the characters possessed by innumerable forms; often even including characters of the great majority of fishes. To be sure, such characters show relationship, but sometimes it is as broad as the relationship of any fish to any other fish. Too often characters possessed in common mean only that their possessors have not departed in respect to them far from some ancestor close to the trunk of the family tree, an ancestor that has given rise to many diverging branches; but the characters are treated as if they indicated a branching far out on the limb.

Still the paradox remains that it is only by resemblances that relationships may be recognized. Among the smaller groups that are usually in question resemblances must be in line with some more or less unique specialization to be of value in classification; something that will distinguish them; that will be a mark of resemblance among the few, but a mark of difference among the many.

Resemblances do not necessarily mean relationship. They may indicate relationship but they do not confirm it. We may have:

(1) Two forms, A and B, that resemble each other very closely in all appreciable respects.

(2) Two forms, C and D, that resemble each other in all respects but perhaps one or two more or less important ones.

(3) Two forms, E and F, that scarcely resemble each other at all.

In each of these three cases conceivably we may have forms with the same degree of relationship.

In the first case, A may be as closely related to B as their resemblance indicates; or, though they may have developed along parallel lines, in actual blood relationship, number of evolutionary generations and space of time that has come between them, they may be no more closely related to each other than E is to F in the third case. In the second case conditions are much the same as in the latter supposition of the first case, but some factor has been introduced that has resulted in a change, making it easier to appreciate degree of relationship and the large number of generations that must have intervened to make the change possible. The third case may indicate simply that E and F have diverged from their parent stem at a greater tangent than the others, and have developed under totally different conditions, but conceivably actual relationship may be as close as in the others.

In most of these cases there is naturally nothing to indicate degree of relationship. Perhaps the examples are exaggerated, but somewhat similar conditions doubtless exist and are among the chief reasons for our inability to design a satisfactory natural classification.

Recently these points were well illustrated by an example of the second case. In working on the osteology of two genera, whose resemblance to each other is so close that the alleged generic differences between them seem to be based on rather unimportant characters, an unexpected difference was found. *Synodus* (four species examined) has no trace of an ossified vomer. *Saurida* (two



species examined) has a well-developed vomer. Considering the apparently close relationship between these two forms this is a most astonishing osteological difference.

No taxonomist examining them externally would think of separating them in groups greater than genera, and yet the absence of a bone so constant as the vomer would usually be considered to mark a family at the least, if not even an order.

As a matter of fact *Synodus* and *Saurida* are probably not so closely related as their resemblance would indicate. Doubtless a vast number of generations come between them, even though in most characters they have been unchanging.

I do not want to discuss here the specific case at hand, but to use it as a particularly good example of a circumstance where the investigator is called upon to decide between two conditions that are more or less opposed to each other. On the one hand, we have a sum of general characters combined with general external appearance; on the other hand, a single osteological character that is of such great importance that it seems to balance the other conditions. We may concede this for the sake of illustration. Hence the question arises: shall we leave the fishes without a vomer in the same family (or larger group) with those with one on account of close general resemblance; or shall we ignore general resemblance, and on account of lack of vomer place them in an entirely different family?

In this case we have a definite character to indicate that possibly these two forms, in spite of their resemblance, are actually very distantly related. Without this one distinguishing character we would have conditions as in the first case and would never question the possibility of their not being closely related.

Consequently, though resemblance may or may not indicate closeness of relationship, we are often driven to its use where there are no other distinguishing characters. That being the case, it seems preferable to give prece-

dence to general appearance; at least giving forms resembling each other the benefit of doubt until they are proved unrelated. Body form and external characters, even scales and fin rays, are, after all, osteological characters.

Some investigators have possessed a feeling for the natural arrangement of groups to a marked degree, and certain relationships that they have indicated, perhaps with little knowledge of internal structure, have with later investigation been verified. Other men, on the contrary, have seized upon a single character that has loomed so large to them that they have ignored all others, together with general appearance and probability, and have used it in placing a group often in a ridiculous and impossible relationship. So the groups have been shifted back and forth, depending upon the opinion of the investigator, with more or less chaotic results.

There is danger in giving undue value to the unfamiliar character or to the character hitherto unknown. Because we are its discoverers, or are the first to point out its condition, we are prone to attach more importance to it than to some character that is so apparent it has been known and used since the time of Cuvier.

Too much rearranging of groups has been undertaken with too meager a knowledge of the value and stability of osteological characters. Often the investigator has examined a single member of a family, basing a definition upon characters that may undergo various modifications within the family.<sup>2</sup>

When we stop to consider that in the single order Nematognathi, or even the single family Characinidae (undoubted natural groups), we have almost as many, and as great, osteological differences as can be found in the whole division of bony fishes, we may well conclude that we know very little of the comparative weight of osteological characters.

<sup>2</sup> The writer wishes to state that in these remarks he has no one definite person in mind, and acknowledges that in many of the points herein criticized he has sinned as deeply as many another.

These groups are held together by a certain few osteological characters of proved value. If such characters did not exist, the osteological differences might well cause us to widely separate them, in spite of the fact that they reasonably could be placed together on account of external resemblances. Such separations have been made in many other groups that have been for years considered naturally arranged. When some osteological character has been found, the value and importance of which its finder had no conception, it has been used as a basis of wide separation and rearrangement, in spite of external characters. Even though external characters are often misleading, existing conditions of arrangement are far more preferable than a change, unless the characters the change is based upon have been widely enough investigated to prove their value beyond doubt.

Surely nothing is gained by placing a lot of forms together and calling them related simply because they have in common some osteological peculiarity the value of which we have no conception of, and which may mean simply a parallel development perhaps caused by a readjustment in the direction of mechanical simplicity. A body compression or depression or shortening or elongation is perhaps followed by a crowding or a pulling apart of the skeletal elements; the excessive development of one bone at the expense of another; some bones lengthening, some shortening, some disappearing, and some getting interpolated between others that are usually in contact with each other; a bone that is crowded out in one form is sometimes doing the crowding in another.

Body form may or may not mean relationship. Eel-like elongation has appeared in many of the diverging lines of descent, just as have Chaetodon-like compression and body shortening, or a tube mouth, or a vertical mouth, the latter often coupled with a sand-burying habit. In many cases we have placed fishes of similar form together, because in looking for characters we find some that are possessed in common. These may go naturally

with body form. For instance, two highly compressed fishes mechanically must have an elongation of the spinous and interspinous elements. Increasing depth changes the angle of the shoulder girdle so that the lower post-temporal limb grows short and the post-temporal is brought in close articulation with the cranium. Similar changes occur in the face bones and other parts, and it is to be expected that fishes of similar body form will have some characters in common.<sup>3</sup> But these may well be only ecological characters indicating mechanical convenience and not necessarily relationship.

Among fishes it is the rule to find the various groups difficult to diagnose and separate sharply. We are usually able to define each group by a combination of characters, especially if we recognize that our definitions are open to some qualifications. It is the exception to find an order or suborder of fishes that can by a single character or combination of a few characters be absolutely separated from other groups. Some, however, may be defined by a single character. For instance, the description, "both eyes on the same side of the head," will separate the flounders absolutely from every other group of fishes.

But where such few groups may be simply defined it is usually because they have developed within themselves some unique character, and with this all the intermediate forms that link them to the main line of descent have disappeared. When no connecting links exist such unique characters show only intra-relationships, and naturally are worthless in showing the stem from which they came. Such characters become exclusive rather than inclusive.

Among the groups that can not be sharply segregated one would imagine for that very reason relationships would be clear, but such is not the case. The intricate, radiating and branching lines of descent are so complex and confused that relationships are obscure even in groups more or less homogeneous within themselves.

<sup>3</sup> In this idea I do not wish to introduce the question of cause and effect. Skeletal modification may follow change of body form or may bring it about, but the results on the problems in hand are the same.

Could we know the true limits and contents of all natural groups we would, of course, have to make exceptions to nearly every character we use in our definitions. It is natural in our conception of evolution that this should be true. Groups can obviously be sharply segregated only by the disappearance of intermediate forms. When these exist the difficulty of segregation by definition becomes more or less impossible. We can not hope to draw sharper lines between the groups than nature does, though this we seem to be forever attempting.

The question then arises: Is it better for the convenience of taxonomy to attempt to make the groups fit our artificial, sharply outlined definitions; or to treat our definitions loosely, recognizing the poorly defined limits of the groups, or, what is more often the case, frankly recognizing our ignorance of the limits and relationships. As it is, we try to do both things—obviously impossible in many cases. In consequence, our schemes of classification, which are bound to be uneven at the best, are more uneven than they have any right to be. In some cases we are able to limit groups to hard and fast lines. In others we either draw loose descriptions or ignore the exceptions to the characters we do use. Thus the percoid fishes and scombroid fishes certainly should be kept separate, but no description has been made that will draw more than an arbitrary line between them. So we keep them separate, remembering the interlocking characters.

We formerly used the suborder *Acanthopterygii* to include all the spiny-rayed fishes that could not be easily segregated. Its contents were arranged in as true sequence as our knowledge and feeling for relationship would permit, and as it was possible to indicate diverging lines of descent by a lineal arrangement of words. Frankly, at the end of the group we placed all those small groups whose place in the scheme was not at all apparent. Recent workers have divided this large loose group into many small ones, separated from each other by more or

less arbitrary and artificial grounds, usually inadequate, many of which will have to be modified for the reception of problematical forms when their relationship in turn shall be guessed at.

To be sure, in using the large suborder Acanthopterygii, we implied our ignorance of the true relationships of its contents, but that was its virtue. It showed a truer condition of things as they are, expressing our inadequate knowledge while it served as a receptacle for all those spiny-rayed fishes whose relationships are not known, and perhaps never can be.

Instead of this frank acknowledgment of ignorance we assume a knowledge that we do not have by basing suborders on trivial characters of unknown value and doubtful meaning, and elaborate combinations of them; using definitions that do not define, and forcing natural divisions with perplexing and vague or incomprehensible boundaries into arbitrary, inflexible and artificial ones. It forces us to place every unaccountable small group into a definite suborder which we have to modify, perhaps, to receive it. On the other hand, when a group can be entirely segregated by an adequate definition into a separate suborder it should be done for simplicity, even though it may not have subordinal weight.

Among the blennies there are several hundred existing species. It is very difficult to divide the subgroups and to appreciate relationship between them, to say nothing of the much more difficult task of appreciating relationships with other groups. But if we add to this great group several other groups that may possibly be related (as has recently been done) the task of defining them as a whole becomes impossible. Of course there is some advantage in thus bracketing groups together to indicate relationship, but the evidence is not at all conclusive that they are related. If, however, we leave them as contiguous groups possible relationship is suggested rather than asserted, and we have a looser, more flexible system, with fewer complications in defining them.



The stand is often taken that a character once lost can never be regained. This may be true, but after a considerable number of years spent in considering the tangle of branches of the fish family tree one can more easily believe the opposite. The supporters of this theory apply it especially to number of ventral rays, though it does not appear why the ventrals should conform to a law different from that governing other fins. However, the theory is very well founded, for in some natural groups the stability in number of ventral rays is surprisingly constant, and though the number may decrease within a group I know of no case that will prove they may be regained. Still this does not prove that ventral rays once lost may not be regained just as they are in other fins. The radial bones at the base of the pectoral fin, the actinosts, one would think would come more surely under this law, but we can scarcely take a similar stand in regard to them. All fishes with an increased number of actinosts most certainly have not retained this character from a primitive ancestor.

Touching this point I would like to quote from a letter that Darwin once wrote to Alexander Agassiz in comment on an address the latter had delivered. I copy it from "Letters and Recollections of A. Agassiz" (p. 162):

I interpreted to myself your remarks on one point in the following fashion. "Any character of an ancient generation or intermediate form may and often does reappear in its descendants after countless generations, and this explains the extraordinary complicated affinities of existing groups."

This idea seems to throw a flood of light on the lines, sometimes used to represent affinities, which radiate in all directions to very distant subgroups—a difficulty which has haunted me for half a century. A strong case could be made in favor of believing in such reversion or atavism after immense intervals of time.

It is bootless to discuss the theory here, but it would go a long way in explaining reasons for many of our difficulties in fish relationship if it could not solve them.

The series of pigeonholes that represents classification were primarily arranged for convenience and order, but

it should beyond dispute be a natural order. Failing this, it should be an unchanging arbitrary order; but the least to be desired is a continually changing order (that is not order at all).

This paper is intended as an argument against the continual change of classification based upon problematical and insufficient characters and upon personal opinion. As it stands, the older investigators, who used only obvious and easily learned characters, have left us a more workable system than have the more recent ones who have relied too much on insignificant or poorly worked out internal characters.

Unless suggested changes show irrefutable evidence of truer relationships we might far better continue the old loose system that served every purpose and conveyed no false conceptions. I believe in the long run our investigations in anatomy will result in a truer arrangement of our pigeonholes, especially if we use the results of our research as added knowledge rather than supplanting knowledge. We are disposed to think first of rearranging a group and then of looking for an anatomical excuse for it. Would not the reverse be more logical? Could we give our anatomical discoveries to the world as such, without so eagerly applying them, would it not be easy for some zoologist of the future to bring them together in a foundation to a classification that could not be changed because it would stand for true relationships.

Recently I had the pleasure of listening to a lecture by Dr. J. C. Merriam in which this thought was suggested (at least to me). The words that conveyed it were doubtless more applicable than these half remembered. "A question would better remain in the form of a question than in the form of an incorrect answer." It exactly fits the case in point.

## BOOKS AND LITERATURE

### SUPPOSED JURASSIC ANGIOSPERMS

MR. H. H. THOMAS has described in a recent paper<sup>1</sup> what he considers to represent a new order of primitive angiosperms. The remains upon which this conclusion is based comprise two somewhat similar types of ovulate fructifications named *Gristhorpia* and *Caytonia*, and a staminate type called *Antholithus Arberi*.

By an ingenious and painstaking method the author has been able to show considerable of the structure of these fossils, which are preserved as inclusions in the middle Jurassic rocks of eastern England. *Gristhorpia* and *Caytonia* show an axis with pinnate megasporophylls of subspherical form enclosing numerous small elliptical seeds. The former are considered to be carpels with a stigmatic flange at the base. The staminate sporophylls show groups of large pollen sacs borne on pinnately arranged branches of a slender axis. The pollen sacs are four winged and contain winged pollen grains like those found on the so-called stigmas of *Gristhorpia*. From association in the rocks the foliage of the plants which bore these ovulate and staminate fructifications is thought to be that known to paleobotanists as *Sagenopteris Phillipsi*.

If botanists are somewhat hesitant in accepting the author's conclusions, this can not detract from the importance of his observations, nor their value in directing attention anew to the old problem of angiospermous ancestry, a problem that has received much speculative and subjective treatment, but practically no elucidation.

In the case of *Gristhorpia* and *Caytonia*, it would seem to the writer that the carpellary nature of the lateral appendages has not been demonstrated beyond all reasonable doubt. The seeds in both cases show a micropylar canal, and in their organization are similar to those seen among the pteridosperms, cycadophytes, ginkgo and gnetum, that is, they are gymnospermous. If, as

<sup>1</sup> Thomas, H. Hamshaw, "The Caytoniales, a new group of angiospermous plants from the Jurassic rocks of Yorkshire." Phil. Trans. Roy. Soc. Lond., B, vol. 213, pp. 299-363, pl. 11-15, 1925.

Thomas supposes, they were enclosed in a carpel, the process of fertilization is somewhat difficult to visualize and is a more complex method than in the gymnosperms mentioned above.

Might it not be possible that the supposed carpel represents an inrolled and reduced pinnule on which these small gymnospermous seeds were borne, and that the supposed stigma represents the puckered tip of such a pinnule, which still left a passageway for the pollen into the interior? If such an interpretation has any basis then *Gristhorpia* and *Caytonia* would represent a new and more advanced as well as younger type of seed fern.

Regarding the correlation of these fructifications with the foliage known as *Sagenopteris*, this is based entirely upon association, an argument often relied upon but one which may be fallacious as Thomas is at pains to point out. If *Sagenopteris* is a seed-bearing plant it would seem that similar fructifications and seeds should occur at very many localities throughout the world at various Mesozoic horizons, for *Sagenopteris* fronds are exceedingly common and widely distributed from the late Triassic through the Jurassic and Lower Cretaceous. So far as known the association described is the only one known.

If Thomas's conclusions are correct then these middle Jurassic plants help bridge the gap between gymnosperms and angiosperms and introduce us to a type which combines fern-like foliage, and gymnospermous seeds enclosed in angiospermous carpels, a most important discovery. The writer hopes that the attractiveness of Mr. Thomas's conclusions will not result in a too uncritical acceptance, and that he will continue his brilliant studies of this intractable material until all doubts regarding his present interpretation shall disappear.

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#### THE OSTEOLOGY OF THE REPTILIA<sup>1</sup>

It is very far from a source of pride to American science that there is no adequate text-book, even approximately up to date, in vertebrate paleontology in the English language. Since the publication of Smith-Woodward's *Outlines of Vertebrate Paleontology*, 1898, and Eastman's translation of the vertebrate portion of Zittel's *Grundzüge*, 1902, there has been no attempt to

<sup>1</sup> By the late S. W. Williston, Harvard University Press.

place such a book before English-speaking students of vertebrate morphology, evolution and geology. The reason is obvious, but this in no wise lessens the need for such a text. American science has contributed its full quota to vertebrate paleontology and there is a reasonable number of students and workers in the field. That the need is felt is shown by the appearance of monographs and books dealing with special phases of the subject. It is to such material that the student and teacher must turn, and extract the necessary synoptic information from a mass of detail. The alternatives are either dreary, detailed lectures and copious notes, or the use of a text-book in a foreign language.

Aside from the necessary inadequate and encyclopedic treatment in certain texts on zoology and natural history, the instructor may place in the hands of the student Dean's *Fishes Living and Fossil*, designedly brief and already very hard to obtain; Gregory's three monographs, the *Orders of the Teleostomous Fishes*, *Present Status of the Problem of the Origin of the Tetrapoda*, and the *Orders of the Mammalia*; Scott's *Land Mammals of the Western Hemisphere*; Osborn's *Age of Mammals*. This is an excellent series but covers the ground only in part. Now we may add Williston's posthumous work, the *Osteology of the Reptiles*.

Only those who know the history of the manuscript of this work will appreciate the debt we owe to the editor, Professor W. K. Gregory, for his sympathetic and masterly work, and to the directors of the Harvard University Press for undertaking the publication. No better hint of the contents can be given than by a quotation from the editor's introduction:

In this book we have the chief results of Williston's half-century of exploration and research in the field of vertebrate paleontology. Here we find the gist of his earlier researches upon the mosasaurs, plesiosaurs, and pterosaurs of the marine Cretaceous of Kansas, the substance of his later and fundamental discoveries among the primitive reptiles of the Permian of Texas, and the epitome of his last comprehensive survey of the evolution of the Reptilia as a whole.

The first part of the book is a comparative summary of the skeletal characters of the various groups of the reptiles, detailing the changes, progressive and adaptive, in the skull, vertebrae, ribs and sternum, girdles and limbs. In this portion the student has the benefit of the author's amazingly detailed knowledge of

the reptilian skeleton and the critical notes of the editor. There are listed 191 figures, but as many carry several figures—there are over 275 in the first 100 listed—the book is an invaluable pictorial atlas as well as a descriptive text.

The second part is a reasoned classification of the reptiles. There can be no more wholesome reading for the student than the introduction to this part of the work. As Williston remarks—no classification does more than reflect the best judgment of an authoritative worker in any field of biology. A thoughtful reading of these pages will go far to rid the student of the conception that every "natural group" is a real thing only waiting to be discovered and described rather than a matter of consensus, or difference, of opinion.

No small part of the value of the book is the reflection of the author's personal opinions and tendencies of thought. Though all may not agree with the conclusions drawn, those who knew Dr. Williston best and appreciate the profundity of learning upon which the conclusions were based will respect them most.

The book fills a great gap in the series of synoptic publications which now take the place of a text-book of vertebrate paleontology in the English language and must speedily find its place as a part of the indispensable equipment of every worker in vertebrate paleontology and morphology.

E. C. CASE



## SHORTER ARTICLES AND DISCUSSION

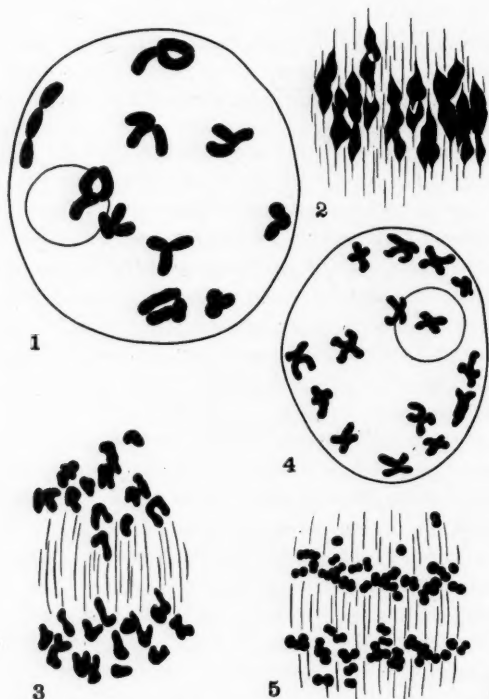
### POLYPLOIDY IN *ZEA MAYS* L.

DURING the course of our investigations on the chromosome numbers in *Zea Mays* a triploid plant has appeared in a culture obtained for cytological and genetical studies from Dr. A. C. Fraser, Cornell University. As compared with the diploid plants of the same culture with their ten pairs of chromosomes, the triploid plant was notably more vigorous; it had a thicker stalk, broader leaves, stouter tillers, larger anthers and distinctly larger microsporocytes. Genetically speaking, the plant appeared to be a dilute sun red with a heterozygous tunicate tassel.

The aceto-carmin method was employed to fix and stain the microsporocytes. Additional material was fixed in other fluids for further study. The history of the chromosome complement was followed from the late prophase of the first meiotic division (*I*) through the second meiotic division (*II*).

On the basis of other evidence not presented here it seems apparent that the basic chromosome number in *Zea* is ten. The plant under discussion possessed thirty chromosomes. At diakinesis these were usually arranged in ten groups of three each, *i.e.*, ten trivalents (Fig. 1). However, in the same preparations a few figures were observed in which the third member of one or more groups appeared unassociated with its homologues. Thus in the same nucleus at diakinesis univalents, bivalents and trivalents were frequently observed.

Fig. 2 illustrates the appearance of the trivalent chromosomes in the metaphase of *I*. (Compare with normal bivalents in Fig. 7.) In early metaphase there are usually ten groups. As in some cases in diakinesis, however, univalents occasionally appeared not clearly associated with any other members of the complement. This suggests a continuous non-association of certain homologues through the late prophase and metaphase. The extra member in each group most frequently appears as if it were united by one end to some point on a normal bivalent, *i.e.*, there is a loose attachment of the third member (see first and last trivalent in Fig. 2). In such a case the third chromosome disjoins from the other two; the latter then pass to opposite poles as usual. In other trivalents of the metaphase complement the three



chromosomes appear to be attached end-to-end with equal closeness. Other modes of association were observed, but whether or not these are characteristic for certain trivalents is not as yet known.

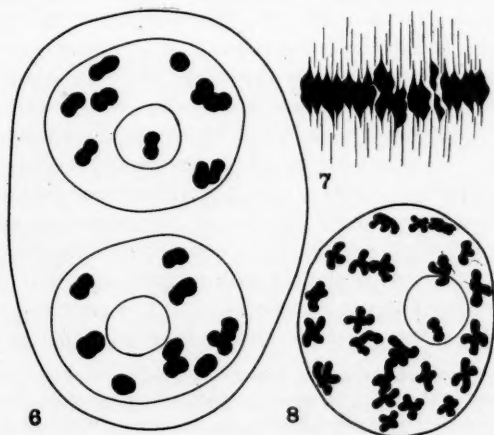
Very early in the anaphase the members of each trivalent appear as three distinct units, and the assortment is apparently a random one. Most frequently, as would be expected, the two anaphase groups show fifteen chromosomes each. However, figures were observed in which the distribution was 14-16, 13-17, and 12-18. In one case the thirty chromosomes were scattered very irregularly between the two poles. It is not known whether this results in the reorganization of one nucleus with the double number of chromosomes, as seems possible from evidence discussed later, or merely indicates a greater delay in the passage of the chromosomes to the two poles.

In the second meiotic division the chromosomes of the prophase are characteristically long and slender, and distinctly X- or

H-shaped (Fig. 4). Here, also, the individual chromosomes are easily distinguishable, sister cells showing most frequently fifteen chromosomes each. Often both mitotic figures were so favorably situated that the number of chromosomes in each anaphase group were countable, so that the number of chromosomes in each microspore of the quartet could be estimated. Occasionally we have observed in one cell, whose size indicates that it is a microsporocyte, a single mitotic figure showing all the characteristics of the anaphase of *II*, but with thirty chromatids in each group (Fig. 5). In case two microspores develop from such a cell, each would contain thirty chromosomes, instead of the usual ten to twenty.

Nothing is known concerning the manner in which triploidy arose in the culture referred to above, but in other cultures the following suggestive phenomena have been observed. In one plant in which many microsporocytes with ten pairs of chromosomes were seen, there were found two binucleate microsporocytes, with ten bivalent chromosomes in each nucleus (Fig. 6), together with a few other microsporocytes showing twenty bivalents in each metaphase of *I* (Fig. 7). In another plant normally showing twelve bivalents in meiosis, cells were observed with twenty-four dyads in the prophase of *II* (Fig. 8), in addition to cells with twenty-four bivalents in the metaphase of *I*. Should viable diploid gametes thus arise, their union with normal haploid gametes would result in a triploid plant.

Since comparatively few cells with the chromosome number thus doubled appear in the anther among normal diploid cells, it



would seem that the former must be due to aberrations occurring in late premeiotic divisions. The occurrence of these various conditions in cells so closely related points strongly toward the conclusion that the stages illustrated in Figs. 6-8 belong to one process responsible for the origin of triploidy, and conceivably of other forms of polyploidy in *Zea Mays*.

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#### THE SIMILARITY OF INSECT FOOD HABIT TYPES ON THE ATLANTIC AND WESTERN ARCTIC COASTS OF AMERICA

THIS paper records the results of a semi-statistical study of the insects collected by the Canadian Arctic Expedition on the western Arctic coast of America and of the insects collected during the course of a survey of the plants and insects of a section of the New Jersey coast, and shows the similarity of the food habit type ratios in each area.

In the "Report of the Canadian Arctic Expedition," 1913-1918 (Vol. III, parts A to K), some 400 species are listed and these were arranged by family units into such groups as phytophagous, saprophagous, harpactophagous, parasitic and miscellaneous. The placing of each family was based mainly on the predominating larval activities of its members. The disadvantages of this method are admitted and have been noted in former papers.<sup>1</sup> In report K of the Canadian Arctic Expedition series, by Mr. Frits Johansen, there is a discussion of the region collected over, the conditions under which the insects were found and of the vegetation insofar as it affected insect life. In view of the availability of this report, it is not necessary to repeat the information here. Many species of plants are mentioned as blooming during the short arctic summer and contrary to general belief, the land is clothed with vegetation at that time.

The section of the Atlantic coast that was surveyed consisted of about ten acres of a strip running from the Atlantic Ocean to

<sup>1</sup> Former papers on the ratios of insect food habits were published in the *Ohio Journal of Science*, Vol. xxiv, pp. 100-106; *Entomological News*, Vol. xxxv, pp. 362-364; *Proceedings Biological Society of Washington*, Vol. 38, pp. 1-4; *Psyche*, Vol. xxxii, pp. 92-94.

Barnegat Bay across Island Beach, New Jersey, about one mile below Seaside Park. Collections by all methods were made throughout the 1924 season and it is assumed that a fair sample of the species present was obtained. The flora of this area was made up of zones or bands paralleling the ocean shore line and was characteristic of a maritime area. Quite a few plants were noted, and although the vegetation was not as profuse as in sections removed from the shore area, it was far from barren and large areas were clothed with vegetation all summer. A more detailed account of the survey of this coast section will be published later.

The orders of insects represented and the number of species found in each is given for each coastal section in the following table.

Order	Atlantic coast number of species	Western arctic coast number of species
Thysanoptera .....	1	0
Collembola .....	0	12
Mallophaga .....	0	20
Anoplura .....	0	3
Hemiptera .....	65	11
Orthoptera .....	17	4
Odonata .....	2	0
Neuroptera .....	2	7
Isoptera .....	1	0
Hymenoptera .....	96	41
Lepidoptera .....	45	121
Diptera .....	93	118
Coleoptera .....	101	65
	423	402

The above species were then arranged according to their family food habits into the groups indicated in the following table. On account of the comparatively small number of insect parasites collected by the Canadian Arctic Expedition, due no doubt to the difficulty of getting a fair sample of small hymenopterous forms on a collecting tour extending over a large territory and lasting only a few hours in some localities, the species of Mallophaga and Anoplura, while not insect parasites, were placed in the group devoted to such species in order to bring the total number in the parasitic group up to a figure more in keeping

with actual conditions. This was the only liberty taken with the species reported from the western arctic coast.

RATIOS OF FOOD HABIT TYPES

	Total number species	Phytophagous per cent.	Saprophagous per cent.	Harpacto- phagous per cent.	Parasitic per cent.	Pollen feeders, misc. species per cent.
Atlantic coast of North America.....	423	45	26	14	11	4
Western Arctic coast of North America.....	402	47	27	14	10	2

The similarity of the ratios shown above for the two widely removed coastal sections is indicative of a more or less fixed relationship between the various types of food habits, this relationship in turn being dependent upon the vegetation, and tends to bear out the suggestion made in previous papers that the relationships between the types of food habits based on the species present, with the numerical ratios between the species and the factors tending to reduce or change their numbers considered as constant, will vary in accordance with the type of vegetation. When small areas, each with a uniform type of vegetation, but differing from each other, are compared, the ratios of the food habit types show a decided variation. When large areas, each embracing different types of vegetation are compared, the variation in the series of ratios appears to be slight.

In other words, in every area, regardless of its size, there appears to be what can be called a fixed set of ratios between the types of food habits, these ratios depending upon the vegetation. If the area is large and embraces different types of vegetation and is considered as a unit, a certain definite set of ratios will prevail. If this large unit is divided into small units, each with a different type of vegetation, the ratios between the types of food habits in the small units will vary in accordance with the vegetation.

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